Fluvial seed dispersal processes and the sustainability of riparian vegetation

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Certificate of authorship of thesis

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Statement of contribution

Because this thesis is written as a series of chapters prepared for publication in peer-reviewed journals, several people other than myself have contributed to the work, and they deserve special acknowledgement. These include:

- Professor Richard Norris: (Institute for Applied Ecology, University of Canberra), who provided guidance and supervision for all aspects for my PhD candidature, and assisted with the preparation of the manuscripts.
- Dr David Williams: (Institute for Applied Ecology, University of Canberra), who provided guidance and supervision for all aspects for my PhD candidature, and assisted with the preparation of the manuscripts.
- Dr Peter Caley: (National Centre for Epidemiology, Australian National University), who provided guidance and advice with R script writing during the development of the semi-empirical model of seed dispersal (Chapter 6).
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These people have been included as authors in the associated chapters and publications, in relation to their respective contribution. However, regardless of contribution, the work that I have submitted is my own, and I have not received any other help apart from that stated above.

As primary supervisor I agree with the above the statement.

Professor Richard Norris Date

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Abstract

Hydrochory, the aquatic dispersal of diaspores, is one method that many species use to extend their range. Fluvial dispersal can transport large quantities of seed hundreds of kilometres through a catchment. Depending on the composition of the seed rain such movement can potentially have detrimental or beneficial effects on the structure of the riparian vegetation. To gain the core knowledge of the dynamics of hydrochory and its potential impact in shaping the riparian vegetation structure, the object of the thesis was *to determine the spatio-temporal patterns of hydrochorous seed dispersal and their sources at the catchment scale.* Incorporated into this theme is that most fluvial seed dispersal occurs during high flow or flood pulses. This study has focused on floating fluvial seed transport in the Wingecarribee catchment.

The aim of this thesis was achieved by sampling the instream species pool with floating aquatic traps and aerial seed rain with bucket seed traps over 17 months; also by surveying the standing riparian vegetation and sampling the soil seed bank upstream from each of the six sites throughout the Wingecarribee catchment, in southeastern Australia. The abundance and richness of the seed rain and soil seed bank was determined by germination trials. To quantify the distance that fluvial seed disperse the dispersal kernel of *Helianthus annuus* (sunflower) achenes along the Wingecarribee River and two of its tributaries was quantified over 24 hrs. Concurrently, the stranding pattern of the achenes were related to abiotic and biotic factors that may influence their aggregation and vegetative cover along the channel banks, while also taking into account seed loss from waterlogging and predation. From the data collected a semi-empirical model of seed dispersal by water was developed, which predicts the parameters of the dispersal kernel.

The instream seed composition varied in relation to the local species, season and water velocity. Over the sampling period, 11 577 viable seeds of 79 species were caught in the instream species pool, with >60% of them being non-native to Australia. Spatial groupings divided the catchment between up and down stream, and secondly between the main channel and the tributary, indicating that at low flow only locally derived species were found in the water column. Similarly there were distinct seasonal changes in the instream seed density and species richness within the catchment, with 30% of it being explained by seed release phenology of riparian vegetation. Increase in water velocity correlated with greater instream seed density (R^2 = 0.62) and species richness (R^2 = 0.25); but seed release

phenology was the main control of the instream species pool, making the river flow regime a secondary influence, showing that the catchment was seed limited. During higher flows seed may be transported long distances from upstream riparian vegetation or be derived from other sources such as the soil seed bank.

The sources of hydrochorous seed and their respective spatial divisions were measured by surveying the standing riparian vegetation, and sampling the soil seed banks and aerial seed rain. A total of 208 species were found from all survey and sampling methods, with 90% of the instream species pool accounted for by the local vegetation and seed banks, indicating that most species were locally derived. Cluster analysis of the species composition found distinct separation between the survey/sampling methods, with secondary spatial separation delineating land use patterns. Furthermore, along the Wingecarribee River there were seasonal shifts in the instream species pool seed source, controlled by the relative seed availability from the standing vegetation and soil seed bank. Large amounts of non-native species found throughout all survey/sampling methods, highlights the need for integrated alien species eradication programs that target not only the riparian zone but also upland vegetation and soil seed banks.

To investigate the dispersal kernel of hydrochorous seed and what factors influence seed aggregation along the banks *Helianthus annuus* (sunflower) achenes were released in three different river reaches. Over 50% of the achenes were deposited within 1000 m and 100 m of the point of release on the Wingecarribee River and its two tributaries respectively, with the furthest being transported 4500 m. At the reach scale (>100 m), water velocity was found to be a significant predictor of the dispersal kernel. At the sub-reach scale (<100 m), all abiotic and biotic variables deemed to influence seed deposition were found to be significant, but were highly variable in causing seed aggregation, with the exception of pool/riffle sequences which consistently indicated that lower water velocity increased deposition.

The core parameters that were quantified from the *H. annuus* release experiment were used to develop a semi-empirical model of seed dispersal by water, which predicts the parameters of the dispersal kernel. The model is based on aerial dispersal and hydrological approaches, with the core parameters a function of flow velocity. Development and calibration of the model has been carried out in the Wingecarribee River and two of its tributaries, through releases of *Helianthus annuus* (sunflower) achenes. The model, of skewed Gaussian form with stream flow and channel dimensions as core parameters,

showed good overall fit to observed (R^2 ranging from 0.61 to 0.98) for the main river and its tributaries. This model increases the fundamental understanding of seed dispersal along rivers and is a tool that can help predict seed dispersal of native and alien plant species along waterways.

This study has shown that hydrochory is an important means for diaspore dispersal for both native and non-native species, and that dispersal varies through time and space. The Wingecarribee catchment was seed limited meaning that the seed release phenology limited seed density and species richness even at high flow. Most seed were locally derived, with water velocity the main influence for the distance they disperse, indicating the importance of flood pulses for the longitudinal connectivity through the catchment. Understanding the magnitude and composition of the seed rain entering a reach will help determine the level of management that may be required for best management practices for river restoration.

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Chapter 1: Introduction: The importance of hydrochory for dispersal and establishment of riparian vegetation

1.1 Background

Adjacent to the river channel is the riparian zone, which is the interface between the aquatic and terrestrial environment and acts as a corridor for abiotic and biotic material through the landscape. Although the riparian zone only accounts for <1% of the landscape it accounts for proportionally more biodiversity (Knopf *et al.* 1988). This is because of its greater fertility, higher water table and soil moisture levels than much of the landscape (Knopf *et al.* 1988; Wallace *et al.* 1997). It also provides fundamental goods and services for humans, such as mitigating non-point pollution, river bank stabilisation, habitat and aesthetics (Hook 2003; Brian *et al.* 2004). Because its productivity and aesthetics are higher than adjacent areas, the riparian zone has been a highly sought after for urban, industrial and agricultural development.

Humans are the main cause of the declining condition of riparian zones (Aguiar *et al.* 2001). Since the industrial revolution, extensive clearing and deforestation of the landscape has occurred, mainly for agriculture and other development. Apart from direct clearing, other cumulative impacts have also diminished the viability of riverine landscapes, included farming practices and industrial pollution. Furthermore, river regulation and channelisation for domestic and agricultural use, change seasonal flow regimes and reduces river connectivity (Andersson *et al.* 2000; Aguiar *et al.* 2001; Pettit and Froend 2001). Genetic continuity between native plant populations is thus reduced, because of the limited number of new propagules entering a riparian stand, and because of reduced inter-patch pollination (Washitani 2001). This lack of continuity leaves endemic populations susceptible to declines in viability.

There are many other human-induced pressures on riparian vegetation. Species that become naturalised are often able to out-compete native species (Benvenuti 2007). This has occurred with the introduction of species such as *Salix fragilis* (crack willow) into Australia, which has no natural predators, and because of its high fecundity has now spread extensively through waterways (Cremer 1999). Likewise, changes to the climate will put pressure on riparian vegetation because of reduced river flows and increase competition for water, resulting in further degradation of riverine communities and reducing connectivity along river systems. To reduce and mitigate against the degradation of riverine

environments there has been new political emphasis on protecting and improving these systems.

The EU (European Union) and USA have both developed water quality policies over the last 40 years, which triggered the inception of broad scale river protection and restoration. Water quality standards were first set in the EU in 1975, focusing on drinking water. The most notable policy change since has been the Water Frame Work Directive (2000), which aims to stop further deterioration of river catchments, and improve all water bodies to a 'good' condition by 2015. To facilitate the directive the rivers are managed at the catchment scale, often across political boundaries, so all degradation and pollution sources can be controlled. The Clean Water Act 1972 was the main USA water policy, one of the priorities of the act was to limit and reduce non-point pollution from agriculture, which helped to instigate restoration and protection of riparian zones. Currently the Clean Water Restoration Act 2009 is passing through congress, which extents the Clean Water Act to all tributaries and wetlands.

Over the past 20 years, within Australia, there have been significant changes in Government policy to better protect riverine environments. Most notably the Water Management Act 2000 (Attorney General of NSW 2000), which was the impetus for the creation of Catchment Management Authorities (CMA) in 2003. In accordance with these policy directives was the Native Vegetation Act 2003 (Attorney General of NSW 2003), which provided a framework for reducing land clearing, conservation of high value areas and restoration of native vegetation. Jointly these policies have been the catalyst for extensive riparian vegetation rehabilitation and revegetation work throughout Australia.

To fulfil the objectives of these policies extensive restoration and revegetation projects have been undertaken. These include invasive weed control, fencing riparian zones and replanting of native species. Extensive resources are invested in this rehabilitation, for example, the Hawkesbury-Nepean Catchment Management Authority spends over $14 m annually on these on-ground projects (Hawkesbury Nepean CMA 2008). However, both nationally and internationally, these revegetation projects often have limited outcomes, plantings fail and aliens become dominant again (Webb and Erskine 2003).

One of the reasons why these rehabilitation works fail is the continued influence of outside seed sources (Webb *et al.* 1999; Levine 2001; Pywell *et al.* 2002). One important seed

source is from fluvially dispersed seed (Andersson *et al.* 2000). An upstream seed source may lead to a continuous flow of alien propagules into a revegetated reach resulting in their germination and thus changing the riparian vegetation structure. Alternatively, fluvially dispersed seed rain may facilitate rehabilitation work by dispersing native plant species through the catchment (Levine and Murrell 2003). Therefore, to better understand population interconnectivity and thus long-term sustainability of riparian plant populations, there is a need to understand fluvial seed dispersal dynamics. However, there has been little Australian and limited international research done on hydrochory.

Seed dispersal research previously has been directed toward quantifying the dispersal kernel of anemochory (wind dispersal) (Okubo and Levin 1989; Greene and Johnson 1996; Clark 1998; Levin *et al.* 2003), and zoochory (animal dispersal) (Leake 1994; Godoy and Jordano 2001; Abe *et al.* 2006). Only relatively recently has this focus shifted to hydrochory (fluvially dispersed seed) (Johansson and Nilsson 1993; Andersson *et al.* 2000; Hampe 2004; Riis and Sand-Jensen 2006), because fluvial seed rain has been shown to be a possible limiting process in structuring riparian vegetation (Levine 2001; Boedeltje *et al.* 2003; Levine 2003; Hampe 2004; Merritt and Wohl 2006). Knowledge of the spatio-temporal fluvial dispersal patterns of diaspores is poorly understood. However this knowledge is needed to better manage and restore riparian vegetation.

1.2 Thesis objective

To measure the spatio-temporal patterns of hydrochorous seed dispersal movement.

The aim of this study is to investigate if hydrochory can help sustain natural patches of riparian vegetation by understanding the factors affecting change in the instream species pool through both time and space. Spatially, to establish variations in the instream species pool in relation to catchment position and adjacent riparian zone seed pools, and determine the dispersal kernel of fluvially dispersed seed. Temporally, to quantify the seasonal changes in seed diversity of the instream species pool, and determine if this relates to any shift in seed source. The spatio-temporal patterns of the instream species pool are also related to geomorphological, hydrological and environmental factors that may control dispersal.

The results of this work will provide an understanding of the long-term sustainability of native riparian vegetation structure. Fluvial seed dispersal may be dominated by non-native species at certain periods or areas within the catchment, thus needing more active management to achieve management goals by comparison with other times or areas when the instream species pool consists mainly of native species. It will provide catchment managers guidance on the areas to target, timing of work and level of management that may be needed to re-establish or protect native riparian vegetation.

1.3 Scope of study

In this study the focus has been on hydrochory in the Wingecarribee catchment. No attempt has been made to predict recruitment of the seed upon deposition. There are many aspects that can limit recruitment such as predation, soil moisture, inter- and intra-species competition, and soil type; such as described by the environmental sieve concept (van der Valk 1981).While many managers want to know if native or alien plants are going to grow in a particular reach, the inclusion of this aspect would have made the project too broad and unachievable within the project time and resources available. Seed composition is an important factor in plant recruitment (Dalling *et al.* 1998), particularly since many rivers are seed limited (Xiong *et al.* 2003).

1.4 Structure of thesis

Following this introductory chapter, the second chapter is a review of relevant published literature on fluvial seed dispersal. The focus of the review is water-borne seed, their source, their life history traits and morphology, their dispersal, and the management implications of hydrochory. Chapters 3 to 6, each answer the main questions that are outlined at the end of Chapter 2 and further quantify the seed inputs and outputs shown in the conceptual model of hydrochory (Figure 1.1).

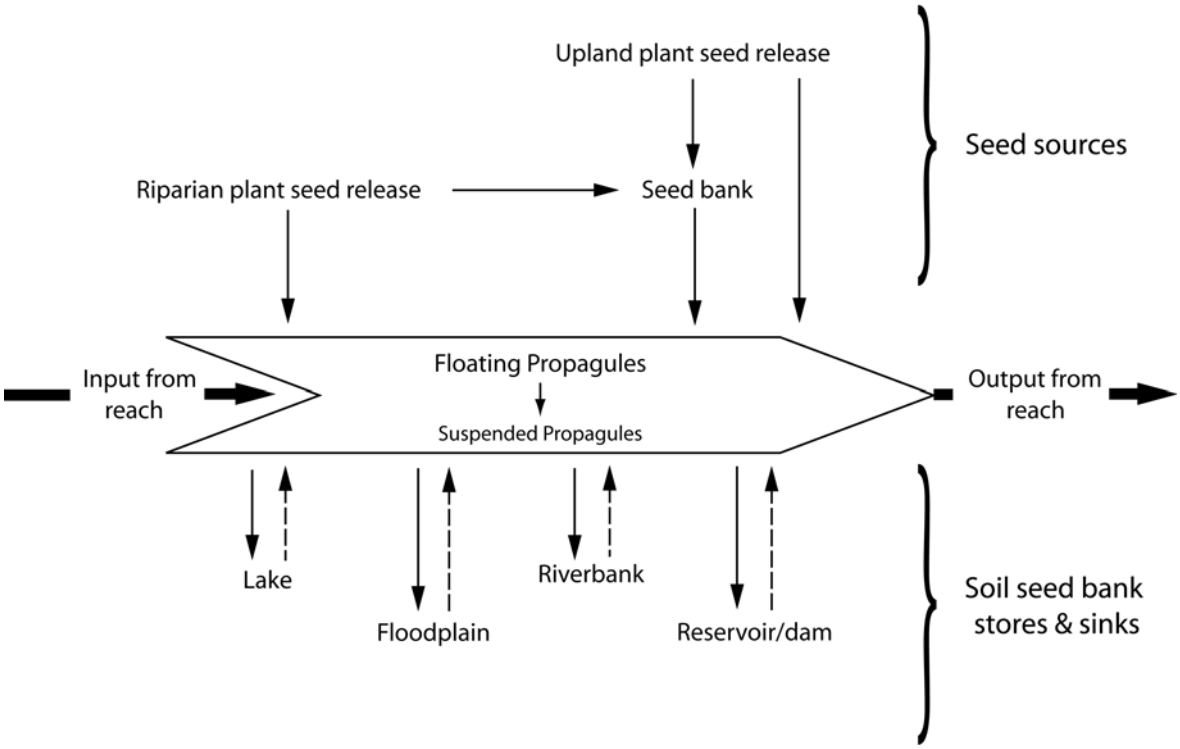

Figure 1.1 A conceptual framework depicting the inputs and outputs of floating diaspores at the reach scale; solid arrows denote primary movement, dashed arrows show possible secondary movement, as determined from the literature, modified from Groves *et al.* (2007).

The chapters are arranged as papers that are either accepted and/or published or are prepared for publication, therefore, there may be some repetition in the methods sections, but every attempt has been made to keep this to a minimum. The synopsis draws the papers together in a general conclusion.

Chapter 3 *Temporal and spatial variability in movement of hydrochorous seeds through catchments* quantifies the spatio-temporal variation in species richness and seed density of fluvially dispersed seed at the catchment scale. Also included is relating the temporal variability of the instream seed composition to the seed release phenology of the riparian vegetation and stream velocity.

Chapter 4 *The relationship between instream species seed pool to three seed sources: soil seed bank, riparian vegetation and aerially dispersal* will investigate the sources of hydrochorous seed. This is done by quantifying species composition of three potential seed sources and comparing this to that of the instream species pool. Also, it will investigate plant life history traits: species origin, life cycle, vegetation type and seed float time in relation to their presence in the instream species pool.

Chapter 5 *Fluvial seed dispersal and the factors that influence deposition and potential loss* will investigate the fluvial disposal curve and the factors causing seed to aggregate in certain areas, while taking into account potential seed loss. Also, investigated is the relationship between seed deposition and riparian vegetation cover.

Chapter 6 *Modelling of floating seed dispersal in a fluvial environment* used the understanding of fluvial seed transport derived from the work reported in previous chapters to develop a semi-empirical model of seed dispersal by water, which predicts the parameters of the dispersal kernel. The model is based on aerial dispersal and hydrological approaches, with the core parameters a function of flow velocity.

Chapter 7 *Synopsis* considers the implications of the work, both theoretical and managerial drawing the four previous chapters together.

Chapter 2: Literature review

2.1 Introduction

Seed dispersal is used by plants to extend their range and maximise recruitment, with outliers possibly transported hundreds of kilometres from their parent source. Even over lesser distances, however, seed dispersal facilitates recruitment by moving seeds to favourable germination environments, reduces intra-species competition and diminishes the risk of predation (Vander Wall and Longland 2004; Nilsson *et al. in press*). The main dispersal mechanisms that are employed by plants are anemochory (wind dispersal) (Clark *et al.* 1998), zoochory (animal dispersal) (Abe *et al.* 2006), autochory (self-propelled dispersal) (Benvenuti 2007) and hydrochory (fluvial dispersal) (Johansson and Nilsson 1993; Andersson *et al.* 2000; Hampe 2004; Gurnell 2007). To optimise their dispersal, seeds are often moved in multiple stages and vectors: firstly, to move away from the parent source and secondly to move to a micro-climate that is advantageous for germination (Vander Wall and Longland 2004).

Understanding of the interconnectivity and long-term sustainability of riparian plant populations may be enhanced by studying hydrochory, namely the dispersal of seeds by water (Nilsson *et al. in press*). Hydrochory is one process that enables plant populations to establish at some distance from their source, and may be important for ecological and genetic continuity between otherwise disjunct populations (Andersson *et al.* 2000). In addition, waterways may be invaded extensively by alien species, which also move down river systems and often out-compete native vegetation, with the potential to change the structure of riparian vegetation (Webb and Erskine 2003; Benvenuti 2007). Therefore, understanding the influences on structuring riparian vegetation, the composition of the upstream species pool, the life history traits of riparian species, and their ability to disperse are important to improve long-term management of this environment.

The aim of this literature review is to give an overview of the spatial and temporal variability of fluvially dispersed seed, and what factors influence changes in their abundance and richness. The review focuses on water-borne propagules, their source, their life history traits and morphology, their dispersal, and management implications of studying hydrochory.

2.2 Water-borne propagules

Aquatic seed traps have been the main method to study temporal and spatial variability in the species richness and abundance of fluvially dispersing propagules (Table 2.1). Stationary instream traps have been used most extensively (Boedeltje *et al.* 2003; Vogt *et al.* 2004; Merritt and Wohl 2006), although methods differ, such as trawling a sampling device behind a boat (Boedeltje *et al.* 2004). Sampling programs have researched temporal variation in instream seed composition from a single site, and spatial gradients over whole catchments (14 sites). Sampling sessions have lasted from 3 days, investigating a single flood (Cellot *et al.* 1998) to up to 5 years (Skoglund 1989). The variety of propagules identified has ranged from 6 to 174 different taxa and up to 360 000 individuals, with both site and seasonal variability in composition and abundance found (Table 2.1).

Temporal variability of water-borne propagules has been found to occur over a flood peak (Cellot *et al.* 1998), over a single thaw (5 months) (Vogt *et al.* 2004), and over multiple seasons (Middleton 2000; Andersson and Nilsson 2002). Within a single year, significant differences in the abundance and richness of propagules were found in the Upper Eider River, Germany; an average of 12 seeds were caught per trap from July to October, whereas >1000 seeds were trapped in August and November (Vogt *et al.* 2004). Likewise, over multiple years, variability between corresponding months was significantly different in the Krycklan River, Sweden, where a 50% reduction in the number of taxa was observed between two consecutive years (Andersson and Nilsson 2002). The change in species richness and abundance that was observed was accredited to seed release phenology, annual seed production and flow levels, although seasonal and river flow changes also accounted for much of the variability in regard to catchment position.

Spatial scale and catchment position has been shown to influence hydrochorous seed composition (Schneider and Sharitz 1988; Cellot *et al.* 1998; Andersson and Nilsson 2002). One project investigated the cross-channel spatial distribution of fluvially dispersed seeds and found that the central two traps, out of a total of four, caught the most seeds, concluding the results were because of higher water velocity in the central streamline (Vogt *et al.* 2004). On a local scale, fluvial seed dispersal was shown to be a second vector of transport, redistributing *Taxodium distichum* (bald cypress) and *Nyssa aquatica* (water tupelo) diaspores to a more favourable position, but only short distances from their parent source (Schneider and Sharitz 1988). At a broader spatial scale, greater species richness

and seed abundance were found downstream rather than upstream in a cut-off channel on the Rhone River, France (Cellot *et al.* 1998). Similarly, at the catchment scale half the number of species were found at the top of the channel than further downstream in the Krycklan River, Sweden (Andersson and Nilsson 2002). The basic premise of these observations was that rivers have good connectivity and that higher stream orders have greater species richness and seed abundance as the river collects biota longitudinally down the catchment, augmented by higher flows (Nilsson *et al.* 1994).

2.2.1 Water velocity influence on instream seed density and richness

The stream flow regime may influence species richness and abundance of water-borne propagules (Nilsson *et al.* 1994; Middleton 2000; Boedeltje *et al.* 2004). A weak relationship was found between water discharge, and both species and seed numbers along the Twentekanaal waterway, the Netherlands (Boedeltje *et al.* 2004). Similarly, during low water flow along the Krycklan River, Sweden, only locally derived species were found in the water column, but during high flow periods propagules were transported from further up the catchment and a greater variety of species was obtained (Andersson and Nilsson 2002). However, extreme events, such as flooding, have shown to be a major driver for the distribution of biota.

Floods are a key driver in propagule dispersal, even though they may occur only a few days per year; they carry most of the biotic and abiotic material that is transported each year (Levine 2001; Pettit *et al.* 2001; Vogt *et al.* 2006). During these high flow events stream power is maximised, which in turn entrains diaspores and other material from the soil seed banks (Goodson *et al.* 2001; Merritt and Wohl 2006; Gurnell *et al.* 2007), and facilitates release of propagules from the surrounding vegetation (Boedeltje *et al.* 2004). Vegetation surveys on the Ume and Vindel Rivers, Sweden, showed the importance of flooding, as more species were found to have established on river meanders and areas that had been flooded (Jansson *et al.* 2005). Alternatively, mimic releases showed that at periods of low flow, diaspores were distributed in a spherical regional pattern; however, after a flood peak the seeds were dispersed further in a more even linear pattern (Middleton 2000). This more even distribution of seeds can be explained by the higher transport capacity of the river; for instance work on the Vindel River showed that the flood peak moved 230 km in 2.5 days, and had the potential to carry propagules with it (Nilsson *et al.*

1994). Source of propagules may therefore be local, during low flow, but may be derived from hundreds of kilometres upstream during high flows.

2.3 Propagule sources

Rivers are important means of connectivity for biotic and abiotic matter, both longitudinally and laterally (Johansson *et al.* 1996; Abernethy and Willby 1999; Levine 2001; Andersson and Nilsson 2002; Nilsson *et al.* 2002; Nilsson and Svedmark 2002; Ward *et al.* 2002; Boedeltje *et al.* 2003). They are often regarded as being unidirectional, transporting propagules from the headwater to the sea. However, lateral and vertical movement may also occur both horizontally between floodplains and the river and vertically up from the groundwater (Johansson *et al.* 1996; Bornette *et al.* 1998; Andersson and Nilsson 2002; Nilsson *et al.* 2002; Nilsson and Svedmark 2002).

2.3.1 Upstream propagule sources

Upstream vegetation influences the propagules that may enter a reach (Honnay *et al.* 2001; Andersson and Nilsson 2002) in cases where alpha diversity, the local species pool, is limited by gamma diversity, the regional species pool (Nilsson *et al.* 1994; Zobel 1997; Baattrup-Pedersen *et al.* 2000; Ward and Tockner 2001; Vogt *et al.* 2004). For instance, species richness was correlated with the upstream species pool, in a vegetation survey along 455 km of the Vindel River, northern Sweden (Renofalt *et al.* 2005). Similarly >71% of the variability of water-borne seeds caught in the Konginsbeek River, The Netherlands, was from the upstream species pool (Boedeltje *et al.* 2003). However, the connectivity with the upstream species pool may be reduced or broken by river regulation.

Table 2.1 Water-borne propagule sampling experiments

Sampling site	[a]Sampling method	Time period (Months)	Sampling interval	No. sites	No. replicates	No. samples	No. taxa	No. individuals	Author
Savannah River, USA	Nets: 75cmx20cm	18	Fortnightly	10	1	180	21	108 233	Schneider & Sharitz (1988)
Lower Dalalven River; Sweden	Plastic box with filter paper disk on the bottom to trap seed: 15x8x5 cm	[b]48/60	[c]Monthly	2	[b]13 - 16	764	23	8 566	Skoglund (1989)
Rhone River, France	Nets: 30 cm diameter, mesh 500 µm	3 (days)	[d]Daily	2	3	36	25	21 041	Cellot *et al.* (1998)
Upper Isar River, Germany	Nets:25 cm wide Mesh:400 µm Basket:30 x 20 x 15 cm^3	7 - 9	Monthly	1	5	Variable	6 - 14	14/210	Bill *et al.* (1999)
Cache River, USA	Seed traps	29	Monthly	6	5	870	20	7 185	Middleton (2000)
Krycklan River, Sweden	Nets:95 x 20 cm Mesh:650 µm	24	Monthly	4	1	216	54	[e]5 000	Andersson & Nilsson (2002)
Koningsbeek River, The Netherlands	Nets:100 x 50 cm Mesh:200µm	12	31 days	1	[f]4 - 5	126	47	106 614	Boedeltje *et al.* (2003)
Upper Eider River, Germany	Nets:16 cm diameter Mesh:100 µm	5	Weekly	1	4	80	75	9 008	Vogt *et al.* (2004)
Twentekanaal, The Netherlands	Nets:30x30 cm Mesh:200 µm Dragged behind boat	12	Monthly	3	1	144	174	359 188	Boedeltje *et al.* (2004)
Cache La Pouder River & South Boulder Creek, USA	Nets:120.4 cm^2 Mesh:25 µm	4	Weekly	11	1	186	[g]22	620	Merritt & Wohl (2006)
Aarhus River, Denmark	Nets: 50 x 70 cm Mesh: 500 µm	7	Fortnightly	1	[f]3	14	N/A	[h]18 - 153	Riis (2008)
Elwha River, USA	Nets: 30.5 x 45.7 cm Mesh: 243 µm	3 (days)	Discrete	2	2-6	53	18	108	Brown & Chenoweth (2008)

[a]Sampled by stationary nets, unless otherwise stated
[b]The two sampling sites were differently treated, for both time period and number of replicates
[c]Monthly only during summer, June to December. During winter they were left and only emptied the next June
[d]Each day two samples were taken sequentially
[e]Maximum per 100 g of litter
[f] One net, replicates were taken one after the other
[h]Range of viable propagules per sample
[g]Identified to family

2.3.2 Regulated rivers

Rivers are defined by the magnitude, frequency, timing, duration and rate of change of their flow. Flow regulation structures change the natural flow regime (Nilsson and Svedmark 2002). River regulation reduces upstream connectivity and transport capacity, resulting in shorter or truncated fluvial seed dispersal (Vogt *et al.* 2006; Brown and Chenoweth 2008). This reduction in connectedness, between upstream and downstream reaches, has the potential to reduce richness along the riparian corridor (Johansson and Nilsson 1993; Jansson *et al.* 2000; Baattrup-Pedersen *et al.* 2005; Jansson *et al.* 2005; Uowolo *et al.* 2005). This was illustrated by the release of rhizomes on the Saver River, where the tail of the dispersal curve did not pass Lake Torrtrasket, showing that the lake acted as a sink. It was concluded that the residence time of the water in the lake and the size of the lake outlet decreased the likelihood of propagules passing through (Johansson and Nilsson 1993). Similarly, sampling of propagules above and below the Glines Canyon Dam, USA, found a significant reduction in species richness and abundance downstream of the structure (Brown and Chenoweth 2008). Alternatively, no statistical difference in species abundance and richness was found comparing a regulated and unregulated river in Sweden (Jansson *et al.* 2005). River regulation structures are known to entrap high proportions of biotic and abiotic material, as found with sediment accumulation, though the ability of many propagules to float may help them to overcome this obstacle (Nilsson and Svedmark 2002; Boedeltje *et al.* 2004).

2.3.3 Lateral propagule sources

Lateral movement of a river into the floodplain influences riparian vegetation structure through both abiotic and biotic inputs (Wissmar 1998; Ward and Tockner 2001; Ward *et al.* 2002; Leyer 2006). This connectedness is described by the flood pulse concept, which predicts that species composition will be determined by flood inundation (Sluis and Tandarich 2004; Renofalt *et al.* 2005). Lateral connectivity is well illustrated by a telescope model (Ward and Tockner 2001), which shows how flooding may cause maximum connectivity laterally from the channel to the bank. As the flood pulse retracts, the areas along the river become less connected, thereby leaving the individual habitats isolated from the channel (Ward and Tockner 2001). However, this idealised concept is theoretical; because the floodplain may not be fully inundated and the different levels of

connectivity to the channel can mean the location of the highest level of species richness and abundance varies between river channels (Ward and Tockner 2001).

Lateral connectivity from upland plants can play a role in the abundance and composition of the riparian zone. Dispersal by other means, such as zoochory or anemochory , as well as by hydrochory from overland flow, can bring propagules into a riparian zone (Garcia-Fayos *et al.* 1995; Pettit and Froend 2001; Renofalt *et al.* 2005). Such a result was found along the Vindel River in northern Sweden, where a strong correlation was observed between upland and riparian vegetation communities (Renofalt *et al.* 2005). An equivalent result was found along the Potomac River, USA (Everson and Boucher 1998). Similarly, propagules were shown to be derived from the floodplain during the summer along the Cole River, UK, which were postulated to have been transported by wind, surface runoff and soil movement (Gurnell *et al.* 2006). Many of the seeds derived from upland areas may be stored temporarily in the seed bank in the riparian zone and later remobilised and transported down the river system.

2.3.4 Soil seed banks

Increases in water velocity has been shown to correlate with increased species richness and seed density (Boedeltje *et al.* 2004). Although the availability of local seed from riparian vegetation may be low, such as during winter, propagules are still found being fluvially transported. Long-distance dispersal may be one source of propagules. Alternatively, it may be from the re-entrainment of temporarily stored propagules from local bank soil seed banks and river substrate (Andersson and Nilsson 2002; Gurnell *et al.* 2008), because at these times higher shear stress is able to remobilise previously deposited propagules. Evidence for these temporary stores has been shown by the high amount of non aquatic species that were found in the substrate, along the Tern and Frome Rivers, UK (Gurnell *et al.* 2007; Gurnell *et al.* 2008). Similarly, riverine seed banks showed they may have acted as temporary stores along the Dove River UK (Goodson *et al.* 2001). Propagules may be sourced from a variety of local and regional sources, both riparian and upland. Therefore, those species that are most suited to surviving multiple phases and vectors of transport have the best chance of more recruitment.

2.4 Plant life history traits and seed morphology

All propagules can disperse by water, but certain life history traits and seed morphologies are advantageous (Johansson and Nilsson 1993; Hancock *et al.* 1996; Naiman and Decamps 1997; Nilsson and Svedmark 2002). Different strategies are needed to optimise and endure hydrochory in different climates; tropical rivers have distinct annual monsoonal peaks, whereas temperate rivers often have variable flood histories (Pettit *et al.* 2001). During dispersal, diaspores can be subjected to extreme conditions, such as freezing, immersion and abrasion. These different conditions may either reduce seed viability or act as a trigger for germination. Therefore, plants use various life history strategies and traits, such as reproductive phenology, seed morphology, and float time to increase their dispersion and viability (Goodson *et al.* 2001).

2.4.1 Seed rain

The species pool and the fecundity of the species are major factors controlling recruitment, because many plant communities are not seed-saturated (Clark 1998; Dalling *et al.* 1998; Boedeltje *et al.* 2003; Bissels *et al.* 2004; Jansson *et al.* 2005). Species abundance within a habitat has been found to correlate with the number of propagules that are available for dispersal (Dalling *et al.* 1998; Boedeltje *et al.* 2003; Boedeltje *et al.* 2004). However, seed rain varies between years because of changes in fecundity and environmental factors (Hampe 2004). Masting years are years of high seed production, with seed production as high as 2 to 10 times that in a normal year (Greene and Johnson 1994; Woolfrey and Ladd 2001). During non-masting years diaspore availability is limited, so plants benefit by abscising their seeds to coincide with periods that may enhance dispersal and recruitment (Titus and Hoover 1991).

Directed seed dispersal, the targeted dispersal of seed though frugivores to a micro-environmental site that is advantageous for germination is used by plants to increase their recruitment. It reduces randomness of the sites seeds disperse to, in comparison to other dispersal methods, by using animal behaviour to transport seed to particular sites. This symbiotic relationship benefits the animal by way of the fruit they eat, whereas, the plant benefits by having targeted dispersal. Mistletoe birds have been shown to disperse mistletoe most effectively to plant stems that were vulnerable to infection (Reid 1989). Similarly, male bellbirds facilitate seed dispersal of many tropical plants to canopy gaps, a

beneficial site for recruitment, in Costa Rica (Wenny and Levey 1998). Directed dispersal is one method that uses animals to target particular microenvironments, whereas other plant species may use environmental queues and dispersal mechanisms to achieve the same goals (Titus and Hoover 1991).

2.4.1.1 *Phenology*

Seasonal timing of seed release can improve a species' chance of dispersal and recruitment in riverine environments (Grubb 1977; Nilsson *et al. in press*). Coincidence of seed release with high flow periods such as snow melt or monsoons enables the species to 'hitch a ride' on the faster moving currents, therefore increasing dispersal (Stainforth and Cavers 1976; Andersson *et al.* 2000; Boedeltje *et al.* 2004; Vogt *et al.* 2004) and fecundity (Pettit and Froend 2001). Dispersal at this time is advantageous as recruitment is facilitated through the occurrence of disturbed patches and increased nutrient levels (Andersson *et al.* 2000; Xiong *et al.* 2001). For instance, phenology of *Carapa guianensis* was studied along the Amazon River where fruit abscised to coincide with the monsoon, germinating within a few days of dispersal (Kubitzki and Ziburski 1994; Scarano *et al.* 2003). Cottonwoods released their seed shortly after annual flood events as the resulting heightened watertable facilited recruitment (Mahoney and Rood 1998). Likewise, seasonal release of *Eucalyptus camaldulensis* seeds was found to correspond with high river flow events (Bren and Gibbs 1986). Recruitment of *Eucalyptus coolabah* corresponded with flood events in eastern Australia (Roberts 1993). In Western Australia, the differences between the phenology of northern (Ord River) and southern (Blackwood River) riparian vegetation were compared; the *E. camaldulensis*, *Melaleuca leucadendron* and *Eucalyptus rudis* on the Ord River were found to release their seeds to coincide with the onset of the monsoon (Pettit and Froend 2001). By comparison, along the Blackwood River, which did not have corresponding annual floods, seeds of *Eucalyptus rudis* were stored on the plant and released over the entire year (Pettit and Froend 2001). The relationship between seed release phenology and flow varies geographically. Environments with succinct seasonal floods often have plants that release their seeds to correspond with flooding, they harness the flow to increase their dispersal potential, whereas species in regions that have variable flood regimes may be serotinous or abscise their seeds to other environmental cues (Boedeltje *et al.* 2004).

2.4.2 Diaspore morphology

Diaspore morphology can impede or facilitate fluvial transport. Size and shape can influence seed dispersal by changing the trapping capacity of seeds. Heavier diaspores may sink and only be transported during periods of higher flows (Cerda and Garcia-Fayos 2002; Riis and Sand-Jensen 2006; Gurnell *et al.* 2007; Gurnell *et al.* 2008). Seed morphology that facilitates wind dispersal is also suited to hydrochory. Seeds that are either plumed (e.g. *Taraxacum, officinale*) or winged (*Acer saccharum*) are also generally light and have a larger surface area, so they are more likely to float or be transported in the water column than sink. Similarly, diaspores such as those from *Casuarina cunninghamiana* (river oak) have small wings (in comparison to its embryo) which limit flight, but aids their buoyancy (Woolfrey and Ladd 2001).

2.4.2.1 *Diaspore buoyancy*

Diaspore floating ability may give a species a competitive advantage, particularly in low water velocity reaches or in regulated rivers (Lundqvist and Andersson 2001; Nilsson *et al.* 2002; Scarano *et al.* 2003; Boedeltje *et al.* 2004). A large variety of seeds are able to float for long periods, such as those of *Carex bigelowii* (Biglow's sedge) and *Angelica archangelica* (garden angelica), which are able to stay buoyant for over a year (Danvind and Nilsson 1997). The benefit of being buoyant was found by comparing a regulated and an unregulated river in Scandinavia. For instance it was shown that the regulated river had lower species diversity, and plants with buoyant diaspores had higher recruitment (Jansson *et al.* 2000). Similar research looking at instream propagules and riparian vegetation along the Krycklan River, Sweden, showed that 48% of the variability in species was explained by the floating ability of the seeds (Andersson and Nilsson 2002). However, non-buoyant or short-floating propagules (<24 hrs) were not so readily transported, except during periods of high flow (Danvind and Nilsson 1997; Jansson *et al.* 2000; Goodson *et al.* 2001; Nilsson and Svedmark 2002; Boedeltje *et al.* 2004). At these times all material in a river has the capacity to be transported (Johansson and Nilsson 1993; Naiman and Decamps 1997; Andersson *et al.* 2000; Jansson *et al.* 2000; Hampe 2004).

There is increasing evidence that in unregulated rivers the ability of a diaspore to float for extended periods does not influence its recruitment (Andersson *et al.* 2000; Jansson *et al.* 2000; Nilsson and Svedmark 2002; Gurnell 2007; Markwith and Leigh 2008). The results

of early studies showed only a weak correlation between floating ability and plant abundance (Johansson *et al.* 1996). However, later work has refuted these earlier claims. Using mimic releases in Scandinavian rivers a correlation was found between stranding position and riparian vegetation cover (Andersson *et al.* 2000). Species richness was greater where mimics stranded, but longer floating species were not necessarily more prevalent, although the authors concluded that recruitment may not be more successful for longer floaters (Andersson *et al.* 2000; Boedeltje *et al.* 2003). Corresponding studies have found similar results with vegetation surveys (Johansson and Nilsson 1993; Jansson *et al.* 2000), and instream seed sampling (Danvind and Nilsson 1997; Xiong *et al.* 2001). The inability of a diaspore to float for a long period does not restrict it from fluvially dispersing (Gurnell 2007; Markwith and Leigh 2008). Non-floating diaspores are able to be dispersed at higher flows, or during flood peaks (Johansson and Nilsson 1993; Hampe 2004). Alternatively, heavier seeds may be trapped and carried with other organic material (Xiong and Nilsson 1997). Species richness and seed density may therefore be limited by a river's flow regime, which controls its carrying capacity, but also its ability to facilitate long distance dispersal.

2.5 Fluvial seed dispersal kernel and deposition

River flow enables transport and exchange of matter, energy and biota between regions, generally described as a linear downstream path (Goodson *et al.* 2003; Boedeltje *et al.* 2004; Sannikov and Sannikova 2007). This capacity of rivers to transport material, including propagules, long distances over short periods means that plant species harnessing this form of dispersal may expand their extent rapidly, which is best visualised by the rapid expansion of invasive species, such as willows (*Salix* spp.).

2.5.1 Distance propagules disperse

To quantify hydrochorous seed dispersal kernel, mimics or tagged vegetative segments have been deployed (Andersson *et al.* 2000; Vogt *et al.* 2004; Riis and Sand-Jensen 2006). These experiments have shown that most seeds disperse short distances, with a few outliers being transported further. For instance, releasing stem fragments in four streams in lowland Denmark showed an exponential decrease in propagule numbers with distance from their release site (Riis and Sand-Jensen 2006). Only 10% of the stem fragments were transported

more than 4.6 km down the river and only 1% reached 9.2 km. Similarly, the release of mimic diaspores, on the Vindel River, Sweden, showed that the seeds could disperse to >150 km over two weeks (Andersson *et al.* 2000). Rhizomes released in the Saver River showed a leptokurtic dispersal, with most found within 1.5 km of the release point, and the furthest found 3 km away (Johansson and Nilsson 1993). The differences in the dispersal curves were attributed mainly to water velocity and channel size.

Fluvial seed dispersal and deposition have shown to be primarily determined by the local flow regime (Schneider and Sharitz 1988; Danvind and Nilsson 1997; Andersson *et al.* 2000; Middleton 2000; Merritt and Wohl 2002; Nilsson *et al.* 2002; Boedeltje *et al.* 2004; Hampe 2004; Riis and Sand-Jensen 2006), with channel roughness (Naiman and Decamps 1997; Andersson and Nilsson 2002; Merritt and Wohl 2002; Nilsson and Svedmark 2002) and seed life history traits (Middleton 2000; Xiong *et al.* 2001; Boedeltje *et al.* 2003) being less important. Water velocity has been shown to be the main driver for fluvial seed suspension and deposition. For instance, a significant difference in seed deposition between low-flow areas (e.g. pools and slack waters), compared with high water velocity areas (e.g. straight reaches and cut banks) was measured (Merritt and Wohl 2002). Similarly, water velocity was the only significant factor that influenced seed deposition in an unregulated Swedish river (Andersson *et al.* 2000). Other studies have shown that microenvironmental factors, such as large woody debris (Johansson and Nilsson 1993; Nilsson *et al.* 1993) and sinuosity (Schneider and Sharitz 1988), can also affect seed deposition, although these associations have not been as well quantified (Andersson *et al.* 2000). Despite this likely influence of microenvironmental factors in a fluvial environment, the broader-scale distribution of fluvially dispersed seed closely resembles that found in anemochory, where water velocity is the main driving force (Greene and Johnson 1989; Johansson and Nilsson 1993; Nathan and Casagrandi 2004), and also the first stage of fluvial point source pollutant transport, where channel dimensions and flow characteristics disseminate the longitudinal dispersal shape (Fischer *et al.* 1979).

2.5.2 Multi-stage dispersal

Seed dispersal is often in multiple stages, with a primary and a secondary stage (Johansson *et al.* 1996; Gordon and van der Valk 2003; Hampe 2004; Vander Wall and Longland 2004; Gurnell *et al.* 2007). The primary stage involves the movement of seed away from the parent plant where there is a large seed bank and therefore high intra-germinant

competition. The secondary stage is the re-entrainment and transport of diaspores either further afield, or to a micro-climate that is advantageous for germination to occur (Gordon and van der Valk 2003; Vander Wall and Longland 2004).

Hydrochory may be the first or second stage of dispersal (Johansson *et al.* 1996; Hampe 2004). Primary fluvial dispersal mainly occurs with aquatic plants such as *Sagittaria* sp. (arrowhead) through the direct transportation of seeds and rhizomes down the channel. Secondary dispersal through hydrochory has been found to be used by terrestrial plants, such as *Frangula alnus* (buckthorn), where primary dispersal was frugivorous (bird dispersed), with the secondary phase dispersed by water (Hampe 2004). However, only one study has investigated diplochory with hydrochory included in one stage (Hampe 2004). This single example is because of the difficulty of studying multiple stage dispersal, and hence most studies have focused on a single dispersal stage (Cooper *et al.* 1995; Vander Wall and Longland 2004; Riis and Sand-Jensen 2006), although the significance of diplochory has been shown through observations (Nilsson *et al.* 1991; Andersson *et al.* 2000; Merritt and Wohl 2002; Gurnell *et al.* 2007). Similarly, fluvial dispersal may extend into multiple stages with repeated periods of transport deposition, storage and re-entrainment before a favourable germination site is found (Johansson *et al.* 1996; Andersson *et al.* 2000; Hampe 2004; Gurnell *et al.* 2007).

2.6 Riparian zone sustainability and revegetation

Plant populations that are reduced below a critical level become caught in a positive feedback cycle. As the population becomes smaller there is an increasing risk of alien species invasion. Increasingly, an endemic population may reach a critical level and enter a 'vortex of extinction'. This is caused by the lack of genetic variability in the community, but also because there are insufficient sexually mature adults for population replacement (Benvenuti 2007). To mitigate community level and species extinction, some level of management is required along river systems.

Long-term viability of riparian zones relies increasingly on greater levels of management (Baattrup-Pedersen *et al.* 2000; Jansson *et al.* 2000; Bischoff 2002; Rood *et al.* 2005; Nilsson *et al. in press*). Such management involves a degree of intervention, either actively or passively. Active management is controlling/manipulating the inputs and outputs into a

region, which includes weeding, planting and maintaining a site (Webb *et al.* 1999; Baattrup-Pedersen *et al.* 2000; Pywell *et al.* 2002; Sweeney *et al.* 2002). Active management has been shown to have worked on a stream restoration project on the Gudena River, Denmark; after two years of work the riparian plant cover had recovered close to pre-restoration levels (Sweeney *et al.* 2002). All too often, however, revegetation projects do not work. A native revegetation project in the Hunter Valley, NSW, failed because of weed re-growth and grazing; it was concluded that these problems could have been mitigated through better understanding of seed inputs and management levels (Webb and Erskine 2003). Similarly, high levels of weed infestation and few native species were found when comparing revegetated sites with reference sites, in the Beaudry Provincial Park, Canada, where it was concluded that more active management was needed to improve the outcomes of revegetation projects (McLachlan and Knispel 2005). Lack of native recruitment often occurs because of a depauperate seed bank and/or the need of seed rain from native species into the area (Dalling *et al.* 1998; Bissels *et al.* 2004). The cost of active management is frequently limiting, thereby necessitating passive management, which can leave areas prone to reinvasion and lower environmental integrity (Bischoff 2002; Sluis 2002). Therefore, knowledge of the temporal and spatial composition and variability of hydrochory in our river systems is an important step toward understanding best management practices for rehabilitation and sustainability of riparian vegetation.

Such a conclusion from the literature forms the background to the study that follows in subsequent chapters of this thesis and addresses the key objective and subsequent questions:

What is the spatio-temporal variability of fluvially dispersed seed in an evergreen habitat in relation to:

1. Species richness and abundance throughout the Wingecarribee catchment.
2. What is the role of the release phenology of riparian vegetation in relation to the abundance and richness of the instream species pool?
3. How does the instream species pool differ from the potential sources of propagules?
4. What is the influence of water velocity in relation to instream seed density, species richness and the seed dispersal kernel?

5. What factors influence fluvially dispersed seed deposition?
6. From the knowledge gained through a literature review and from primary data, is it possible to develop a semi-empirical model that describes the dispersal curve of fluvially dispersed seed?

Chapter 3: Temporal and spatial variability in movement of hydrochorous seeds through catchments

This manuscript is ready for submission to the journal 'Freshwater Biology'

Groves J.H., Williams D. G., Norris R. H. Temporal and spatial variability in movement of hydrochorous seeds through catchments

3.1 Summary

1. Fluvially dispersed seeds can be transported hundreds of kilometres through a catchment. Depending on the composition of the seed rain, such movement can potentially have detrimental or beneficial impacts on the structure of the riparian vegetation.

2. Understanding the spatial and temporal variation in fluvial seed dispersal at the catchment scale can help improve both management and rehabilitation of riparian vegetation.

3. Variability in instream seed density and richness was measured transversely across the channel at three sampling sites, to quantify the best sampling position. Using floating seed traps the fluvial seed rain was sampled each month for 17 months at six sites in the Wingecarribee catchment, southeast Australia. Concurrently, bucket traps were used to measure the aerial seed rain that was dispersing into the river system. The abundance and richness of the seed rain was determined by germination trials.

4. Over the sampling period, 11 577 viable seeds of 79 species were caught in the instream species pool, with >60% of them being non-native to Australia. Water velocity was the main influence on cross-channel seed density, but centrally located traps better captured a representation of all locally derived seed. Spatial grouping divided the catchment between up and down stream representing land use patterns, and secondly between channel size. Similarly, there were distinct seasonal changes in the instream seed density and species richness within the catchment, with 30% of it being explained by seed release phenology of riparian vegetation. Higher water velocity correlated with higher instream seed density (R^2 = 0.62) and species richness (R^2 = 0.25), but seasonal availability limited instream seed density and species richness.

5. Diaspore release phenology was the main control of the instream species pool, with the river flow regime a secondary influence, showing that the catchment was seed limited. Distinct spatial separation of the instream seed composition was found within the catchment indicating that at low flows mainly locally derived species were found in the water column. During higher flows seed may be transported long distances from upstream vegetation or derived from other sources such as the soil seed bank.

3.2 Introduction

Hydrochory, the dispersal of seeds by water, is a transport vector that can influence riparian vegetation structure by the quantity and variety of species that are transported into a reach (Vogt *et al.* 2004). Both alien and native species can be dispersed hundreds of kilometres through a riverine environment (Andersson *et al.* 2000). The amount of seed rain from a particular species or from a few outliers, that become established kilometres from their parent source, can change riparian vegetation structure by increasing a species dominance within a region (Andersson and Nilsson 2002). Although there are large scale riparian revegetation projects, both within Australia and internationally, knowledge is lacking on hydrochorous seed rain dynamics, which has implications for long-term plant population dynamics and community structure.

There are many studies that have sampled water-borne propagules in the northern hemisphere. Sampling has generally been done by placing nets in the channel without quantifying the proportion of seed being collected in relation to the entire river cross-section (Andersson and Nilsson 2002; Boedeltje *et al.* 2004; Vogt *et al.* 2004; Merritt and Wohl 2006). For example, Boedeltje *et al*. (2004) sampled instream propagules 2 m from the bank in a 40 – 60 m wide canal, along the Twentekanaal waterway, The Netherlands. Sampling at different levels of the water column showed that >70% of the seed were transported either near or on the surface of the river (Merritt and Wohl 2006). One project that investigated the cross-channel spatial distribution of fluvial seeds found that the central two traps, of a total of four, caught the highest numbers of seeds (Vogt *et al.* 2004). They hypothesised that this was because of the cross-channel velocity profile. Although transverse channel factors such as the water velocity profile and position of seed deposit in the channel may influence the capture rates for both seed density and species richness, they have not been quantified previously. Quantifying the distribution of fluvial seed across the channel will more accurately depict the spatial temporal variation of hydrochorous seed at the catchment scale by defining a sampling protocol that captures the best representation of the instream species pool.

Upstream vegetation influences the seed that may enter a reach (Honnay *et al.* 2001). Both alpha diversity (upstream species pool) and gamma diversity (or catchment diversity) restrict the abundance and richness of seed that may occur in the water column (Nilsson *et al.* 1994; Zobel 1997; Baattrup-Pedersen *et al.* 2000; Ward and Tockner 2001; Vogt *et al.*

2004). A positive relationship was found between the change in local vegetation richness in relation to the upstream species pool from a vegetation survey along 455 km of the Vindel River, northern Sweden (Renofalt *et al.* 2005). Consequently, even though a reach may be located on a higher order stream, the richness and abundance of the instream seed rain may be poor because of the lower vegetation cover upstream.

Seed release phenology can improve a species' chance of dispersal and recruitment in riverine environments (Grubb 1977; Mahoney and Rood 1998; Seiwa *et al.* 2008). Coincidence of seed release with high flow periods such as snow melt or monsoons enables seed to harness higher flows and thus disperse further (Stainforth and Cavers 1976; Andersson *et al.* 2000; Boedeltje *et al.* 2004; Vogt *et al.* 2004) and thereby increase their recruitment (Pettit and Froend 2001). Dispersal at this time is advantageous because recruitment is facilitated through the occurrence of disturbed patches and increased nutrient levels (Andersson *et al.* 2000; Xiong *et al.* 2001). For instance, the phenology of *Carapa guianensis* was studied along the Amazon River where fruit abscission coincides with the monsoon, and germination occurs within a few days of dispersal (Kubitzki and Ziburski 1994; Scarano *et al.* 2003). Likewise, seasonal seed releases of *Eucalyptus camaldulensis* (Bren and Gibbs 1986), *Eucalyptus coolabah* (Roberts 1993) and *E. camaldulensis*, *Melaleuca leucadendron* and *Eucalyptus rudis* (Pettit and Froend 2001) corresponded with high flow events. However, comparing northern and southern Australian riparian vegetation, *E. rudis* seeds were found to be stored on the plant and released over the entire year in non-monsoonal regions (Pettit and Froend 2001). Reductions to the natural flow regime, however, can be potentially detrimental to fluvial dispersal by reducing the ability of seed to be transported.

The flow regime may influence species richness and abundance of water-borne seed (Nilsson *et al.* 1994; Middleton 2000; Merritt and Wohl 2002; Boedeltje *et al.* 2004), as predicted by the flood pulse concept (Junk *et al.* 1989). A significant relationship was found between discharge, and both species richness and seed number along the Twentekanaal waterway, The Netherlands (Boedeltje *et al.* 2004). Similarly, during a period of low flow along the Krycklan River, Sweden, only locally derived species were found in the water column, but during high flow periods seed were transported from further up the catchment and a greater variety of species was obtained (Andersson and

Nilsson 2002). Thus sources of seed during higher flow events are potentially from upstream sites or temporary instream stores.

Higher species richness and seed densities found during floods and higher water velocity may arise from seed being remobilised from the seed bank or river substrate because of the higher shear stress (Goodson *et al.* 2001; Boedeltje *et al.* 2004; Gurnell *et al.* 2007). Evidence for these temporary stores has been shown by the high numbers of non-aquatic species which were found in the substrate along the Tern and Frome Rivers, UK (Gurnell *et al.* 2007). Similarly, riverside seed banks showed they may have acted as temporary stores along the Dove River, UK (Goodson *et al.* 2001). Therefore, during seasons normally having low seed abscission, increased water velocity may result in augmentations to seed density and species richness in the water column.

In this paper the temporal and spatial variability of fluvially dispersed diaspores are investigated. It was hypothesised that at the catchment scale composition will be locally derived, with long distance dispersal only occurring during high flows periods as described by the flood pulse concept, but will be limited by the upstream riparian composition and seasonality. At the reach scale, the hypothesis is that seed release phenology and river velocity will control the seed composition variability. Specifically, our research questions are: (1) Is there variance in cross-channel density of fluvially dispersed seed? (2) What is the temporal and spatial variability of fluvially dispersed seed density and species richness? (3) Does the temporal pattern of instream seed density correlate with seed release phenology? (4) Does instream species richness and seed density correlate with fluvial processes?

3.3 Methods

3.3.1 Study site

The study area was in the Wingecarribee catchment in southeastern Australia (Figure 3.1). The catchment is 700 m above sea level with an area of 763 km^2. The main channel is 80 km long, averages 20 m wide, and descends >300 m from the Wingecarribee reservoir to the confluence with the Wollondilly River. The river networks are highly channelised with steep banks and escarpments. Near the confluence with the Wollondilly River the channel runs through a series of sandstone gorges.

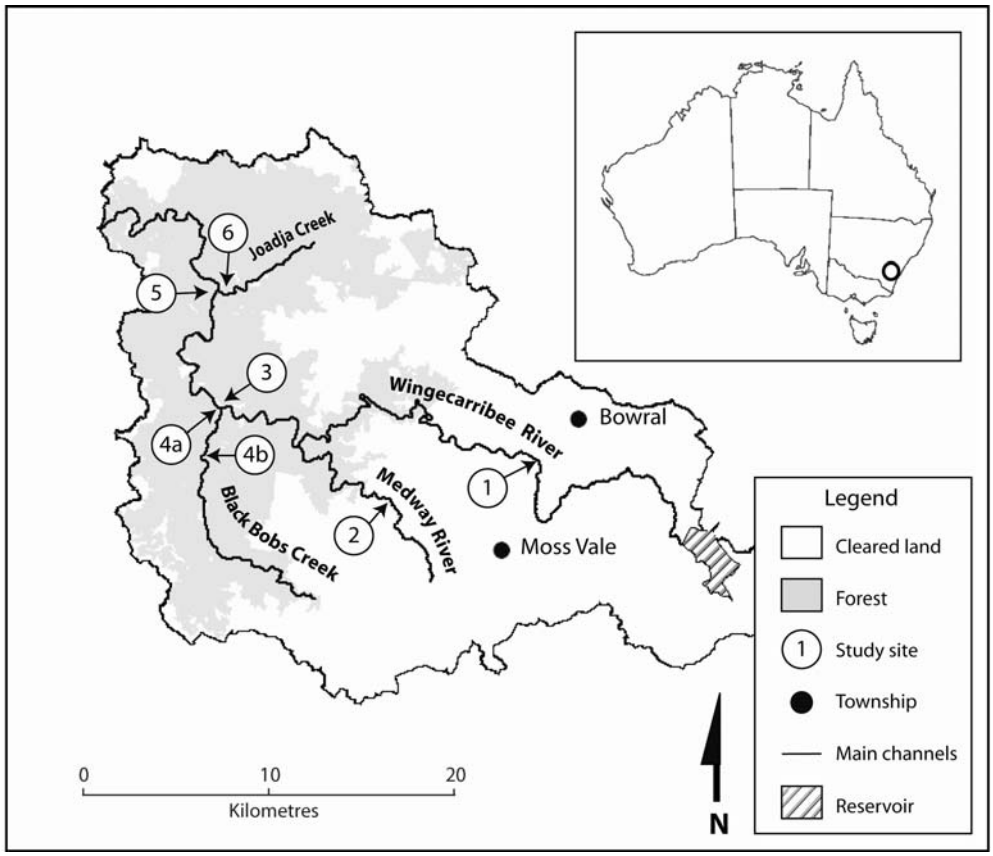

Figure 3.1 Location of study sites in the Wingecarribee catchment, New South Wales, Australia. The sampling site on Black Bobs Creek was originally 200 m upstream from the confluence with the Wingecarribee River (site 4a); however, because of upstream development and riparian rehabilitation works, the site was moved (July 2007) 5 km up the creek (site 4b)

The Wingecarribee River is used for inter-basin transfers for Sydney's water supply, resulting in the flow regime being controlled by releases from the headwater dam. The average discharge is 454 MLd^{-1} and fluctuates between 12 MLd^{-1} and 10 000 MLd^{-1}. Land use within the catchment is divided into two major regions. The upper catchment has been extensively cleared and developed, consisting mainly of grazing land and urbanised areas. The riparian zone (30 m from bankfull) has <50% tree cover and is generally open to stock and human access, with intermixed patches of pasture grasses and species of *Eucalyptus*, *Leptospermum* and *Salix*, with *Crataegus monogyna* (hawthorn) and *Rubus fruticosus* (blackberry) the main introduced woody weeds. The lower catchment has >50% riparian zone tree cover and has more native tree and shrub cover consisting mainly of *Eucalyptus, Acacia, Leptospermum* and *Casuarina* species.

Sample sites were located longitudinally down the Wingecarribee River with sites 3 and 5 located immediately upstream from sampling sites in reciprocal tributaries (Figure 3.1). The Medway Rivulet sampling site (site 2) was located 7 km from the confluence with the Wingecarribee River on a 4th order reach within cleared farmland. The rivulet is 17 km, with an average width of 4 m and an average discharge of 0.08 m^3s^{-1}. The sampling site at Black Bobs Creek was originally located on a 5th order reach, 200 m upstream from the confluence with the Wingecarribee River (site 4a). However, because of upstream development and riparian rehabilitation work, the site was moved (July 2007) 5 km up the creek (site 4b). Black Bobs Creek is 18 km, with an average width of 3 m and an average discharge of 0.05 m^3s^{-1}. It is surrounded mainly by grazing land, although much of the lower channel is fenced off from stock access. Joadja Creek site (site 6) was on a 4th order reach located 0.3 km upstream from the confluence with the Wingecarribee River. The creek is 8 km, with an average width of 5.6 m, and an average discharge of 0.2 m^3s^{-1}.

3.3.2 Variability in instream diaspores with river cross section

To determine the variability in cross-channel density of fluvially dispersed seed, *Helianthus annuus* (sunflower) achenes were released upstream from a chain of traps placed across three of the sampling sites. The release sites were on the Wingecarribee River (site 3), Black Bobs Creek (site 4) and Joadja Creek (site 6) (Figure 3.1).

The traps were made from 500 μm mesh, with an opening of 0.3 x 0.15 m and a cone-shaped tail 1 m to the apex. At the apex of the cone removable sampling jars were attached to the nets so that they could be unscrewed for total evacuation of the nets' contents. The *H. annuus* achenes that were used in the release were first sterilised by heat and then colour-coded to distinguish between replicates.

At the Wingecarribee River site 10 nets were placed across the river. Netting (500 μm) covered the gaps between the individual nets. The release site for the *H. annuus* achenes was located 50 m upstream from the nets. The cross section at the release site was divided into 1/3 intervals and 3 replicates of achenes were released at each interval 15 minutes apart. Prior to the release, the water velocity profile and stream dimensions were measured in front of the nets at 1/10 intervals of the river width. Water velocity was measured using a velocity meter (FLO-MATE 2000) and the river dimensions calculated with a total station (Leica TCR407). The nets were collected after 2 hours and the number of achenes in each was counted.

The variance in the cross-channel density of the fluvially dispersed seed was measured in the tributaries in a similar manner to that used for the Wingecarribee River. However, because the channel width was considerably narrower, only the central channel position was used as a release point for the three replicates. Likewise, because of the narrower channel width, four and three nets were used to block off the channel along Black Bobs Creek (site 4) and Joadja Creek (site 6) respectively. The nets were retrieved after 24 hours, to coincide with other experiments that were taking place at the time.

3.3.3 Instream sampling

Instream sampling of fluvially dispersed seed was carried out once a month for 17 months at each site in the Wingecarribee catchment (Figure 3.1). Two nets, as previously described, were placed with one in the highest water velocity section of the river and the other in the centre of the channel, reflecting the outcome of the variability in instream diaspores derived from the river cross section trail. Each net was left for five hours at each site. The nets were positioned in the water so that 2/3 of the net opening was under water, thus sampling the top 100 mm of the river and ensuring that all floating seeds were trapped. Concurrently with the sampling, the stream dimensions and water velocity were measured (see previously). The samples were taken back to the laboratory, dried, cold stratified at 4 ^{o}C (14 days), weighed and stored until the germination trials commenced.

Flooding during June 2007 restricted safe access to most of the sampling sites and therefore only the Wingecarribee River site 5 was sampled normally. The other two sites along the main river (sites 1 and 3) and on Medway Rivulet (site 2) were sampled from the side of the channel; Joadja Creek and Black Bobs Creek were not sampled.

Seedling germination trials were used to determine the species richness and abundance of the collected instream samples. Sterilised sand was used as the base and an even layer of debris was spread over 0.4 m^2 trays. The two samples from each site were mixed and then re-divided into two subsamples. One treatment was watered daily and the other was submerged under 5 cm of water (Brock *et al.* 1994). If the amount of debris that was collected was >1 L a second tray was used. Alternatively, if the sample was <0.01 L only a watered treatment was germinated.

The samples were planted out in September of each year (2007 and 2008) for the respective sampling periods, and removed the subsequent February. The glasshouse was

watered for 15 minutes each day from an automatic system; the glasshouse temperature was maintained at 24^{o}C during the summer by evaporative cooling. As seedlings emerged they were identified and removed. Those species that were not identified at the end of the experiment were re-potted and grown on until they flowered. Plant identification was done using the Flora of NSW (Harden 1990 - 1993) and any further verification was carried out at the Australian National Herbarium, Commonwealth Scientific and Industrial Research Organisation (CSIRO) Plant Industry, Canberra.

3.3.4 Aerial seed rain

Aerial seed rain was measured with bucket seed traps immediately upstream from sampling sites 1 – 4 (Figure 3.1). The seed traps were made from a funnel, with an opening of 255 cm^2, and mounted in an upside down bucket with a hole in the bottom (Cottrell 2004). Cloth bags were attached to the funnel spout to collect the seeds that were captured by the funnel. Ten replicate seed traps were placed at each site. The other two instream sampling sites were not used because of limiting access agreements with the landowner. The bucket traps were placed directly upstream from the instream sampling sites, at random sites 50 m apart. They were emptied once a month coinciding with the time of instream sampling. Although they were attached to the ground with pegs, both cattle and wombats occasionally knocked them over. The samples were taken back to the laboratory and the number of seeds counted.

3.3.5 Data analysis

The effect that water velocity, cross-channel net position and transversal seed release position had on the capture rate of the nets was quantified by calculating the odds ratio (SPSS v16). The exp(β) parameter estimate shows that for every unit increase in the odds ratio there is an equal rise in the chance of seed deposition (versus non-deposition) between the net positions. Therefore, an odds ratio of 1.0 indicates the variable had no influence on seed position in the channel, while a variation larger than ± 1 demonstrates a large difference. An odds ratio of >1.0 indicates a positive influence and <1.0 a negative. The data were weighted by the number of achenes that were deposited in each net. The covariates were water velocity and net position, and for the Wingecarribee River, release position. The odds ratio was calculated for each site separately.

Descriptive statistics were calculated to describe the results from the instream sampling. Instream seed density (m^3s^{-1}) was calculated from the watered treatment. No significant difference in species abundance was gained by using the submerged treatment as <10% of total germinants were derived from this treatment. Therefore using this treatment to calculate seed density would result in underestimating the number of viable seed that may germinate the riparian zone (Gurnell *et al.* 2007).

The variability in species abundance and richness between catchment position and seasonality were investigated using two-way parametric analysis of variance (ANOVA) Seed density (m^3s^{-1}) was log transformed to comply with the assumption of homogeneity of the variances. For the purpose of the analysis upper catchment position was defined by sites one and two, which had low riparian tree cover (< 50%), and the other four sites as lower catchment sites, with high riparian tree cover (> 50%). High seed release periods were from February to June as defined by the temporal pattern of the aerial dispersed seeds caught in the bucket seed traps, and the other months were the low periods.

To understand the spatial and temporal relationships of community structure, agglomerative hierarchical cluster analysis based on Sorensen's distance measure (PC-ORD 4) was calculated. Ten uncommon species (<10 diaspores) and eight samples which had zero germinants were removed from the analysis. The data were relativized (p = 1) so that species abundance for each sample was proportional to the sample total. The analysis categorised common assemblages between similarities in the instream diaspore species composition in relation to their spatio-tempo variability. The groups were identified by number and the percent of sites that corresponded to each spatio-tempo grouping were calculated. Plant species that were most influencial in separating the groups were identified through indicator species analysis.

To calculate the relationship between water velocity, and seed density and richness of fluvially dispersed seed, linear regression was used. The dependent variable was water velocity and the independent variables were seed abundance and richness. To identify outliers Cook's distance was used. The main outliers were derived from the June 2007 flood and high autumn seed densities. All models were reported, both with and without outliers. To understand the general relationship between seed release phenology and instream seed pool density Pearson's correlation coefficient was calculated.

3.4 Results

3.4.1 Variability in instream diaspores with river cross section

Stream velocity and achene release position both significantly influenced the number of seeds that were caught in the nets (Table 3.1). Along the Wingecarribee River release position also influenced the variety of achene colors that were caught in the trap. Net 1, positioned in the highest water velocity stream line, caught the most achenes. However, they were all from the left hand release position, whereas the other nets caught achenes from at least two release positions (Figure 3.2).

3.4.2 Variability in hydrochorous seed composition

A total of 79 species and 11 577 viable seed were trapped at the six instream sampling sites over 17 months (Table 3.2). More than 60% of the species that were dispersing were non-native to Australia, with significantly more being dispersed down the main channel than down the tributaries ($p < 0.001$, $F = 49.652$, df = 1, 200), but no difference between upper and lower catchment sites ($p < 0.115$, $F = 2.502$, df = 1, 200). However, non-native species consisted of <50% of the total number of germinants. The most abundant species that were trapped were *Casuarina cunninghamiana, Conyza bonariensis* and *Rumex crispus*, which made up 56% of the total number of seeds collected from all the sites. Overall, the 10 most abundant species made up 77% of the seed rain within the catchment (Table 3.2) although only half of these common species were derived from all the sites. For many of the most abundant species the majority of the seeds were derived from only one or two sampling sites, e.g. *Ludwigia peploides* was mainly collected from site 1 (72%), *Verbena bonariensis* predominantly from site 3 (90%) and *Casuarina cunninghamiana* seeds were nearly all derived from sites 3 and 5 (96%). Overall, 30% of the species that were trapped were found at only one of the sampling sites.

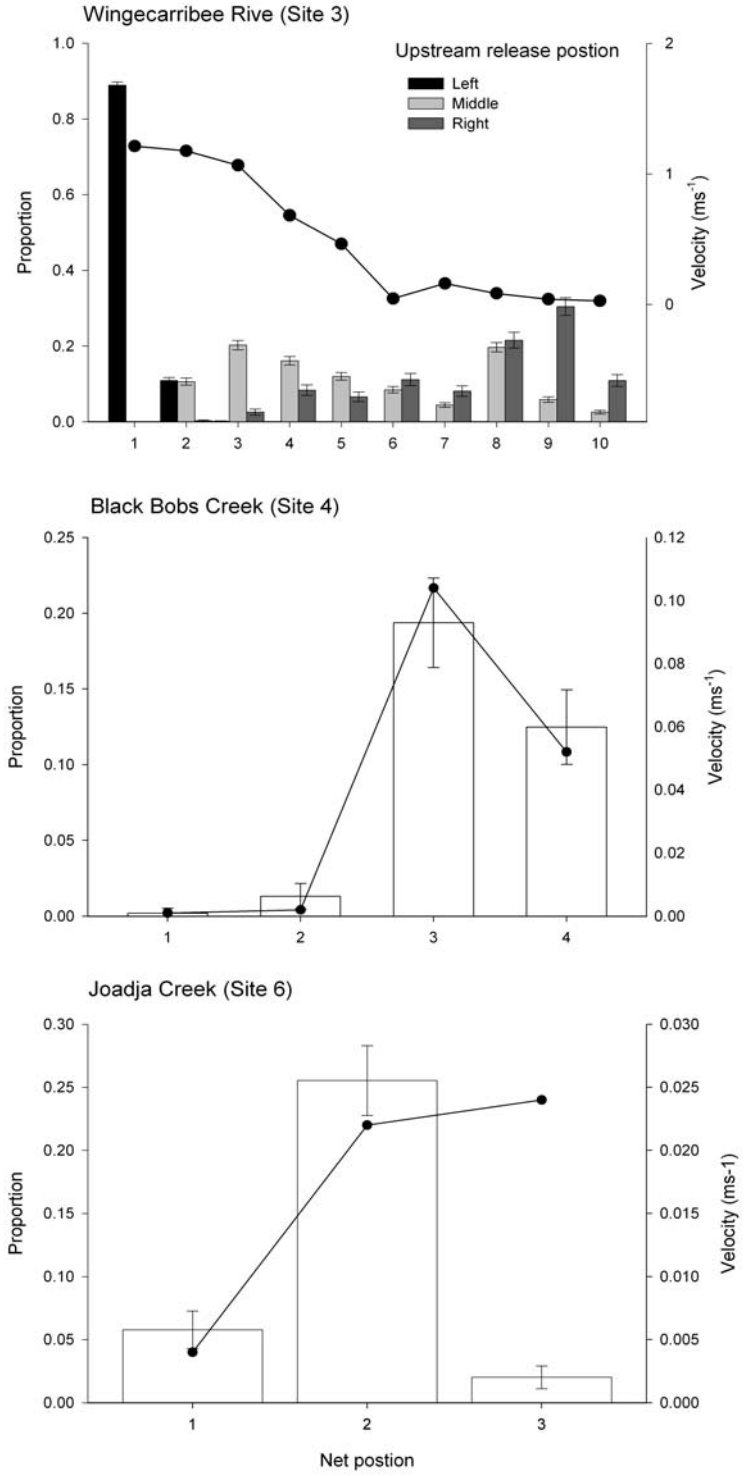

Figure 3.2 Cross-section distribution of *Helianthus annuus* achenes and water velocity profiles measured at three sampling sites within the Wingecarribee catchment. The release of the *H. annuus* achenes was located 50 m upstream from the nets. Along the Wingecarribee River (site 3) the transect was divided into 1/3 intervals and 3 replicates of achenes were released at each point. However, only the central channel position was used as a release point for the three replicates along the two tributaries (Sites 4 and 6).

Table 3.1 The influence of water velocity, net position and release position on channel transversal seed density in the Wingecarribee River (site 3), Joadja Creek (Site 4) and Black Bobs Creek (Site 6); summarised are the results from the logistic regression model: model logistic regression coefficient (β), standard error (S.E.), Wald statistic (Wald x), significance level (*P*), the odds ratio (Exp(β)) and their confidence intervals

						95.0% C.I. for exp(β)	
Site Variable	β	S.E	Wald x	*P*-value	Exp(β)	Lower	Upper
Wingecarribee River (Site 3)							
Water velocity	0.952	0.035	722.116	<0.001	2.592	2.418	2.778
Net position*	-0.370	0.026	202.761	<0.001	0.691	0.657	0.727
Release position*	-0.645	0.025	659.800	<0.001	0.525	0.500	0.551
Black Bobs Creek (Site 4)							
Water velocity	3.373	0.425	62.863	<0.001	29.175	12.672	67.169
Net position§	3.249	0.422	59.205	<0.001	25.775	11.265	58.975
Joadja Creek (Site 6)							
Water velocity	-57.828	15.598	13.744	<0.001	0.000	0.000	0.000
Net position§	3.375	.267	159.412	<0.001	29.234	17.311	49.367

*Gradient runs from the left hand side of the channel cross-section
§Gradient is from the centre of the channel

Sites along the Wingecarribee River had >100x the number of seeds (m^3s^{-1}) and 2x the number of species, compared to the levels in the tributaries (Figure 3.3). The average numbers of species were similar between the sites (11.7, SE 0.5) down the Wingecarribee River; however, the lower catchment site (site5) had an average of 50% less diaspores (m^3s^{-1}) than the upstream two sites (Figure 3.3). The periods of highest seed dispersal were during late summer through to early winter. During the peak period >6x the number of seeds and twice the number of species were transported through the Wingecarribee catchment (Figure 3.3).

Differences in the instream species pool between catchment position and season were analysed using a two-way ANOVA. A significant difference in species richness was found between the Wingecarribee River and the three tributaries ($p < 0.001$, $F = 34.744$, df = 1, 92) and between high and low seed release periods ($p < 0.001$, $F = 26.105$, df = 1, 92), but not between upper and lower catchments ($p = 0.22$, $F = 1.519$, df = 1, 92). Analysis of species abundance (m^3s^{-1}) showed a similar pattern with significant differences were found between the main channel and the tributaries ($p = 0.007$, $F = 7.485$, df = 1, 92) and between high and low seed release periods ($p = 0.002$, $F = 1.080$, df = 1, 92), but no significant difference was calculated between sites longitudinally down the catchment ($p = 0.003$, $F = 0.598$, df = 1, 92). Analysis using each sampling site as the dependent variable showed the same spatio-temporal division within the catchment (not shown).

Table 3.2 Species and their proportional abundance collected in aquatic seed traps from six sampling sites, also total viable seed and species relative occurrence, which relates to the species abundance in comparison to all other species collected in the Wingecarribee catchment, southeastern Australia; sampling was carried out monthly from March 2007 to August 2008, species identification and counts were from germination trials

	Relative occurrence per site						Total	Relative
species	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	seed count	occurrence per species
Alternanthera denticulata	7.5	7.8	30.1	10.2	12.6	31.7	372	3.21
*Anagallis arvensis**	50.0	0.0	0.0	0.0	50.0	0.0	2	0.02
*Anthoxanthum odoratum**	0.0	0.0	0.0	0.0	100.0	0.0	2	0.02
*Bidens pilosa**	12.5	50.0	0.0	25.0	0.0	12.5	8	0.07
*Bromus catharticus**	48.7	1.3	34.6	5.1	6.4	3.8	78	0.67
*Bromus hordeaceus**	100.0	0.0	0.0	0.0	0.0	0.0	12	0.10
Cadamine paucijuga	0.0	81.8	13.6	0.0	0.0	4.5	22	0.19
*Carduus tenuiflorus**	0.0	0.0	75.0	0.0	0.0	25.0	4	0.03
Casuarina cunninghamiana	0.1	0.1	73.9	0.3	21.9	3.7	4023	34.75
Centipeda minima	0.0	98.9	1.1	0.0	0.0	0.0	93	0.80
Cerastium glomerata	70.6	0.0	29.4	0.0	0.0	0.0	17	0.15
*Chamaesyce maculata**	12.9	0.0	17.2	14.7	37.9	17.2	116	1.00
*Chenopodium ambrosioides**	80.0	0.0	0.0	0.0	0.0	20.0	5	0.04
*Chenopodium pumilio**	25.0	0.0	12.5	37.5	25.0	0.0	8	0.07
*Cirsium vulgare**	7.4	7.4	44.4	0.0	11.1	29.6	54	0.47
*Conyza albida**	1.1	0.0	98.9	0.0	0.0	0.0	90	0.78
*Conyza australis**	0.0	100.0	0.0	0.0	0.0	0.0	7	0.06
*Conyza bilbaoana**	100.0	0.0	0.0	0.0	0.0	0.0	2	0.02
*Conyza bonariensis**	2.5	0.2	72.7	0.0	11.7	12.9	1672	14.44
*Conyza canadensis**	0.7	19.2	39.7	0.0	36.7	3.7	297	2.57
*Cynodon dactylon**	83.3	16.7	0.0	0.0	0.0	0.0	12	0.10
Cyperus difformis	28.6	16.1	26.8	7.1	17.9	3.6	56	0.48
*Cyperus eragrostis**	42.8	11.0	16.5	2.9	23.1	3.8	346	2.99
Cyperus lucidus	26.7	0.4	72.9	0.0	0.0	0.0	225	1.94
Cyperus sphaeroideus	0.0	0.0	33.3	0.0	66.7	0.0	3	0.03
*Dactylis glomerata**	38.2	5.5	5.5	21.8	14.5	14.5	55	0.48
Dichondra repens	0.0	0.0	20.0	0.0	10.0	70.0	10	0.09
*Digitaria sanguinalis**	0.0	1.5	93.2	0.0	5.3	0.0	133	1.15
Einadia nutans ssp. *nutans*	52.4	21.9	24.9	0.3	0.5	0.0	370	3.20
Eleocharis sphacelata	75.0	0.0	0.0	0.0	0.0	25.0	4	0.03
*Eragrostis curvula**	0.0	0.0	0.0	0.0	100.0	0.0	5	0.04
*Fumaria muralis**	0.0	0.0	0.0	0.0	100.0	0.0	1	0.01
Galium migrans	91.5	0.4	5.1	0.0	2.9	0.0	272	2.35
Geranium solanderi	25.0	75.0	0.0	0.0	0.0	0.0	4	0.03
*Gnaphalium americanum**	57.1	0.0	28.6	14.3	0.0	0.0	7	0.06
*Hirschfeldia incana**	0.0	0.0	100.0	0.0	0.0	0.0	3	0.03
*Holcus lanatus**	42.0	32.0	11.0	7.2	5.5	2.2	181	1.56
Hypericum japonicum	0.0	0.0	0.0	0.0	100.0	0.0	1	0.01
*Hypochaeris radicata**	0.0	83.3	8.3	0.0	0.0	8.3	12	0.10

Table 3.2 (continued)

species	Relative occurrence per site						Total seed count	Relative occurrence per species
	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6		
Isolepis inundata	35.7	10.1	31.0	8.5	6.2	8.5	129	1.11
*Juncus articulatus**	6.6	4.4	1.1	3.3	2.2	82.4	91	0.79
*Juncus capitatus**	0.0	100.0	0.0	0.0	0.0	0.0	12	0.10
Juncus usitatus	0.0	0.0	100.0	0.0	0.0	0.0	1	0.01
*Lactuca sativa**	0.0	7.7	92.3	0.0	0.0	0.0	13	0.11
*Lactuca serriola**	0.0	66.7	0.0	0.0	0.0	33.3	3	0.03
*Lolium perenne**	77.8	11.1	11.1	0.0	0.0	0.0	9	0.08
Lomandra fluviatilis	80.0	0.0	20.0	0.0	0.0	0.0	5	0.04
Lomandra longifolia	16.7	16.7	33.3	16.7	16.7	0.0	6	0.05
Ludwigia peploides	71.5	2.2	11.7	0.0	11.9	2.7	411	3.55
Lycopus australis	100.0	0.0	0.0	0.0	0.0	0.0	11	0.10
Microlaena stipoides	100.0	0.0	0.0	0.0	0.0	0.0	6	0.05
*Modiola caroliniana**	0.0	100.0	0.0	0.0	0.0	0.0	3	0.03
*Nassella trichotoma**	25.0	0.0	0.0	0.0	75.0	0.0	4	0.03
*Oxalis corniculata**	22.2	11.1	11.1	19.0	22.2	14.3	63	0.54
Oxalis perennans	0.0	0.0	0.0	0.0	100.0	0.0	4	0.03
*Oxalis pes-caprae**	0.0	0.0	12.5	0.0	0.0	87.5	8	0.07
*Paspalum dilatatum**	5.9	2.9	26.5	52.9	8.8	2.9	34	0.29
Persicaria hydropiper	33.2	2.6	35.9	3.3	16.8	8.2	304	2.63
*Persicaria maculosa**	0.0	0.0	0.0	0.0	100.0	0.0	11	0.10
Persicaria prostrata	0.0	0.0	0.0	0.0	100.0	0.0	1	0.01
Phragmites australis	100.0	0.0	0.0	0.0	0.0	0.0	21	0.18
*Plantago lanceolata**	25.0	68.3	6.7	0.0	0.0	0.0	60	0.52
Poa labillardieri	100.0	0.0	0.0	0.0	0.0	0.0	4	0.03
*Poa pratense**	52.6	0.0	0.0	15.8	31.6	0.0	19	0.16
*Polycarpon tetraphyllum**	0.0	0.0	0.0	0.0	100.0	0.0	1	0.01
*Pontederia cordata**	20.0	40.0	20.0	0.0	20.0	0.0	5	0.04
Pratia purpurescens	100.0	0.0	0.0	0.0	0.0	0.0	1	0.01
*Romulea rosea**	0.0	100.0	0.0	0.0	0.0	0.0	9	0.08
*Rorippa palustris**	50.7	13.3	8.7	2.7	20.0	4.7	150	1.30
*Rubus fruiticosus**	66.7	0.0	0.0	0.0	22.2	11.1	18	0.16
Rumex brownii	13.5	16.3	37.6	5.0	14.2	13.5	141	1.22
*Rumex conglomeratus**	41.8	5.1	27.8	13.9	7.6	3.8	79	0.68
*Rumex crispus**	50.8	10.5	23.6	1.0	10.1	4.0	800	6.91
*Rumex obtusifolius**	55.0	6.3	20.0	0.0	15.0	3.8	80	0.69
*Scirpus polystachus**	0.0	0.0	0.0	0.0	100.0	0.0	1	0.01
*Solanum nigrum**	0.0	0.0	28.6	0.0	50.0	21.4	14	0.12
*Sonchus asper**	4.7	5.7	54.7	6.6	12.3	16.0	106	0.92
*Trifolium repens**	16.2	16.2	10.8	10.8	21.6	24.3	37	0.32
*Verbena bonariensis**	4.1	3.1	89.9	0.0	0.6	2.2	318	2.75
Proportion of seed per site	29.8	15.8	21.6	3.9	20.8	8.1	11 577	

*Non-native species to Australia

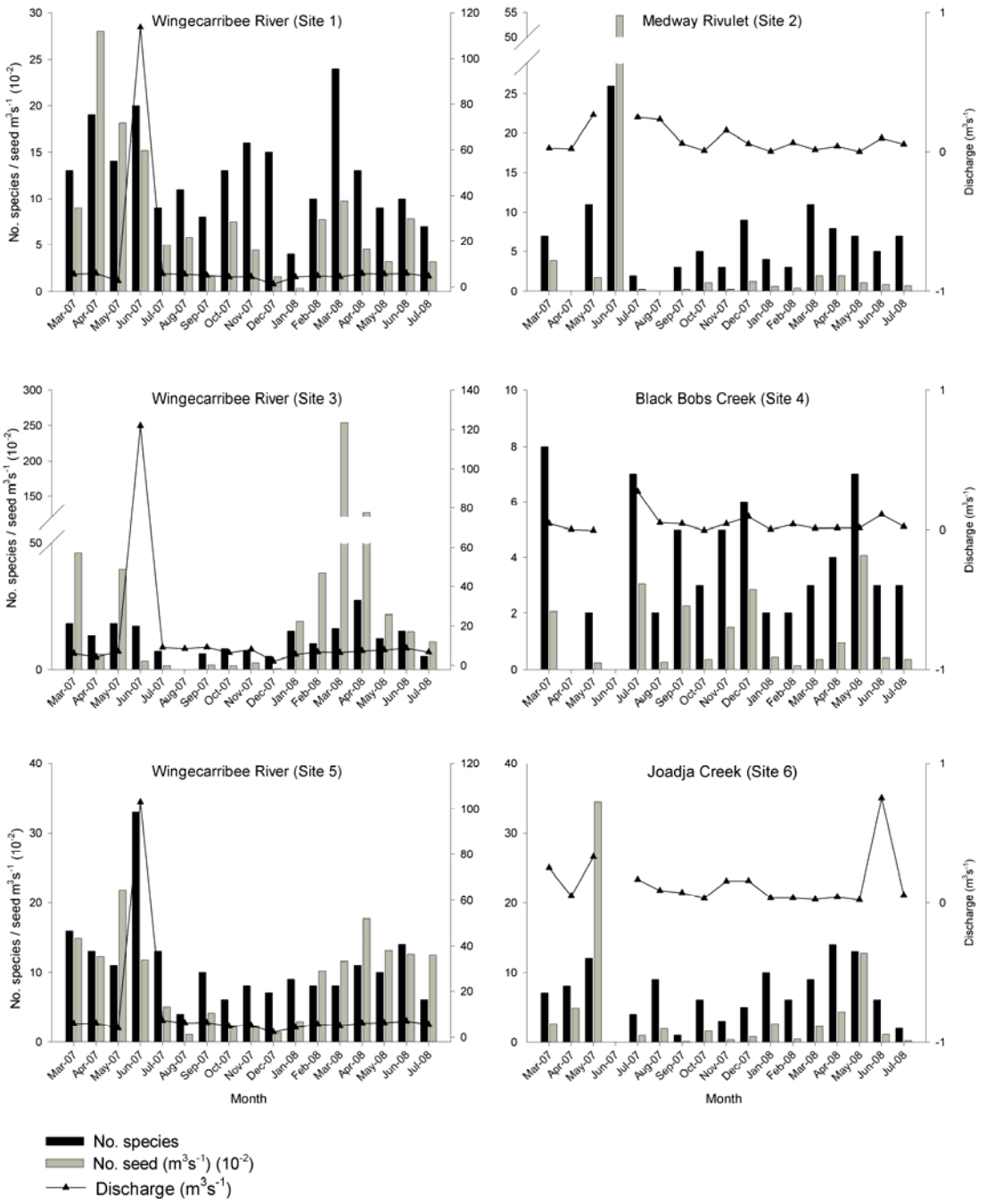

Figure 3.3 The variation in species richness and seed abundance (m^3s^{-1}) (10^{-2}) of fluvially dispersed seed, and water velocity from monthly sampling at six sites in the Wingecarribee catchment, southeastern Australia; flooding during June 2007 restricted sampling, and therefore only the Wingecarribee River (site 5) was sampled normally. The other two sites along the main river (sites 1 and 3) and on Medway Rivulet (site 2) were sampled from the side of the channel and Joadja Creek and Black Bobs Creek were not sampled

Species composition data were grouped through the use of cluster analysis, based on Sorensen similarity index (Figure 3.4). The cluster groups are referenced by number. These numbers are set against spatial and temporal variables, which showed a distinct spatial separation between upper and lower catchment position, and between the main channel and the tributaries (Figure 3.4; Tab le 3.3), and the indicator species (Table 3.4). Similarly, seasonal shifts distinguished cluster groups, with subsets delineated for groups four and five (‘a’ & ‘b’), showing that there were distinct seasonal patterns in the seed that were being dispersed through the catchment.

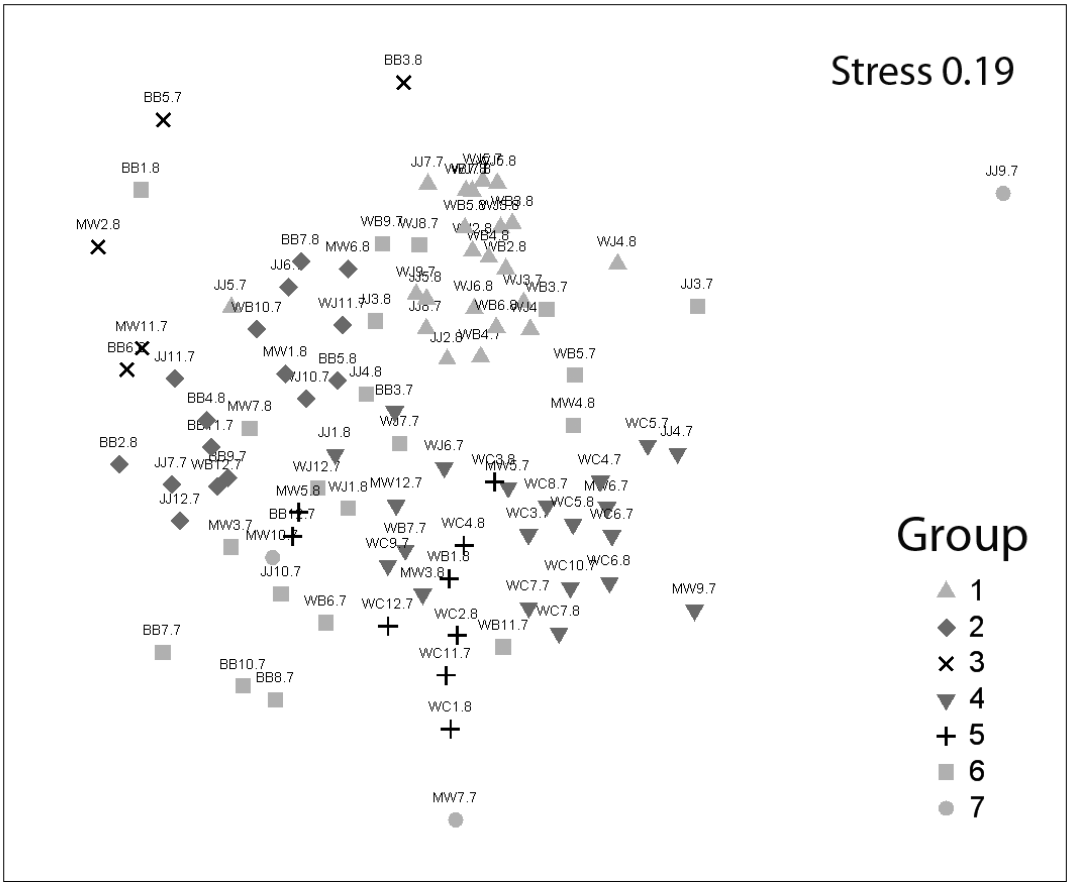

Figure 3.4 Ordination based on standardized abundance of instream seed composition between six sites over 17 months within the Wingecarribee catchment. Southeastern Australia; groups 1 – 7 are the main groups delineating catchment position and season (Table 3.3)

Table 3.3 Spatio-temporal characteristics of instream species pool from the Wingecarribee catchment, southeastern Australia; each group is shown as proportion occurrence in relation to the equivalent variable, derived from the cluster analysis (Figure 3.4)

Catchment position	Channel size	Release period	Classification group								
			1	2	3	4a	4b	5a	5b	6	7
No. observations			22	16	5	9	12	4	5	20	3
Lower			100.0	87.5	60.0	11.1	33.3	25.0	20.0	85.0	33.3
Lower	Wingecarribee R.		77.3	25.0			16.7	25.0		45.0	
		*High	63.6				8.3			15.0	
		*Low	13.6	25.0			8.3	25.0		30.0	
Lower	tributaries		22.7	62.5	60.0	11.1	16.7		20.0	40.0	33.3
		*High	13.6	25.0	60.0		16.7			15.0	
		*Low	9.1	37.5		11.1			20.0	25.0	33.3
Upper				12.5	40.0	88.9	66.7	75.0	80.0	15.0	66.7
Upper	Wingecarribee R.					55.6	50.0	75.0	60.0		
		*High				11.1	41.7	75.0			
		*Low				44.4	8.3		60.0		
Upper	tributaries			12.5	40.0	33.3	16.7		20.0	15.0	66.7
		*High		6.3	20.0	22.2	8.3		20.0	10.0	
		*Low		6.3	20.0	11.1	8.3			5.0	66.7

*High: February – June; Low: July – January

3.4.3 Relationship between seed release phenology and instream seed density

Patterns of abundance of aerial and fluvial seed rain patterns were similar within the Wingecarribee catchment. The average aerial seed rain had up to 20x the number of seeds (m^2/month) during autumn in comparison to the other seasons. No significant difference was found between sampling sites ($p = 0.479$, $F = 0.84$, df = 3, 48), but significant different was established between seasons ($p < 0.001$, $F = 16.975$, df = 3, 48). The correlation between aerial and fluvial seed dispersal was significant ($R^2 = 0.36$, $F = 33.1$, $P = <0.005$).

3.4.4 Water velocity influence on instream seed density and richness

Water velocity significantly influenced seed density and species richness within the Wingecarribee catchment (Table 3.5). Flood events and seasonal peaks increased instream seed density and species richness causing significant outliers as defined by Cooks' Distance. After eliminating these outliers, a weaker relationship was found for seed density, but little difference for species richness.

Seasonally there was a clear relationship between water velocity and seed transportation (Table 3.5). The weakest correlation for seed density and water velocity was during

autumn, which may relate to the availability of seed at the time. The strongest correlation between flow and seed density occurred in winter. However, taking into account the flooding at the beginning of the season, water velocity accounted for only 40% of variability in seed density, which is comparable to that found during the other seasons.

Table 3.4 Indicator species for each group (Figure 3.4), which had >70% abundance and >50% frequency, derived from cluster analysis

Group	Species
1	*Conyza bonariensis*
	Casuarina cunninghamiana
2	*Rumex crispus*
3	**Chamaesyce maculata*
	**Verbena bonariensis*
4A	*Adiantum aethiopicum*
4B	*Cyperus difformis*
	Oxalis corniculata
5A	*Cyperus eragrostis*
	Cyperus lucidus
	Phragmites australis
	Persicaria hydropiper
	Galium migrans
5B	*Bidens bipinnata*
	Rumex brownii
6	*Rorippa palustris*
	Einadia nutans ssp. *nutans*
	Ludwigia peploides
7	*Bromus catharticus*
	Dactylis glomerata
	Holcus lanatus
	Poa pratense

*Indicator species, but <70% abundance and <50% frequency

Table 3.5 Relationship between water velocity and instream seed density (A) and species richness (B) in the Wingecarribee catchment, New South Wales, Australia; summarised are the regression models for all sampling times, also shown are models excluding outliers caused by a flood event and extreme seasonal values; the results presented are the regression model, their fit and significance levels

		All sampling					Outliers removed				
Seasons	Seed	a	b	R^2	*F*-ratio	*P*-value	a	b	R^2	*F*-ratio	*P*-value
All	[1]Density	-0.011	0.198	0.627	166.155	<0.005	§ -0.001	0.013	0.319	42.538	<0.005
	[1]Density						* 0.001	0.179	0.126	13.352	<0.005
	Richness	7.696	1.314	0.247	32.092	<0.005	§ 5.318	5.135	0.255	31.089	<0.005
Summer	[1]Density	-0.130	0.145	0.365	9.208	0.008					
	Richness	5.248	4.657	0.252	5.388	0.034					
Autumn	[1]Density	-0.006	0.385	0.158	6.393	0.016	§ -0.005	0.201	0.566	41.773	<0.005
	Richness	6.776	8.425	0.419	24.564	< 0.005	§ 6.857	7.403	0.403	21.585	<0.005
Winter	[1]Density	-0.084	0.202	0.778	94.727	< 0.005	* -0.003	0.064	0.437	16.324	0.001
	Richness	6.278	1.279	0.465	22.590	< 0.005	* 3.586	3.948	0.279	8.100	0.010
Spring	[1]Density	0.000	0.043	0.359	8.947	0.009					
	Richness	3.717	5.199	0.488	15.259	0.001					

[1]Number of seeds (m^3s^{-1})
*Regression without the flood of June 2007 (Cook's Distance)
[§]Regression excluding outliers caused by flood and extreme seasonal values (Cook's Distance)

3.5 Discussion

3.5.1 Variability of instream diaspores with river cross section

In relation to our first research question, the highest water velocity stream line, in comparison to the cross channel water profile, significantly influenced the proportion of seeds that were caught per net (Figure 3.2; Table 3.1), as previously postulated (Vogt *et al.* 2004). This was probably because seeds become entrained in the fastest stream line reducing transverse mixing (Fischer *et al.* 1979), as found in the Wingecarribee River where >90% of the left hand released *H. annuus* seed were deposited in the corresponding downstream left hand net (Figure 3.2), whereas, the other two release positions, which were released in lower water velocity streamlines, had greater transversal mixing represented by the more dispersed distribution across the channel of achenes captured in the down stream nets. Therefore if the cross channel water velocity profile at the sampling point is skewed toward one bank, the highest abundance of seed will be caught in the highest streamline, but centrally located traps within the channel cross section may better represent all locally derived seed.

Achenes released on Joadja Creek (site 6) had the lowest achene recapture rate in the nets in the highest water velocity. This may have arisen because of overhanging vegetation that influenced the surface hydrology just upstream from the net deflecting the seed toward the central net (observational only). This illustrates how other factors may also influence the net capture rate at a particular position, the need to undertake preliminary sampling and understand the cross-section distribution of seed at each sampling point.

3.5.2 Spatial variability in hydrochorous seed composition

Instream species composition was grouped into high/low catchment categories with secondary groupings separating the main channel and the tributaries through cluster analysis (Figure 3.4; Table 3.1), indicating that most species were locally derived. Local disposal was further indicated by the most abundant species being trapped only at a single or a few sites, such as with *Casuarina cunninghamiana* (Table 3.2). Furthermore, seed abundance and species richness did not show successive increases down the Wingecarribee River during low flow events (Figure 3.3). There was no significant difference in the species number or variation between the tributaries, which represent various catchment

sizes and flow rates, signifying the channels were not accumulating species and long distance dispersal was not occurring at this time. Propagule release experiments have shown that most propagules disperse short distances at low flow (Johansson and Nilsson 1993; Riis and Sand-Jensen 2006). Similarly, local hydrochory was found for flood drift line deposits (Vogt *et al.* 2006) and instream sampling (Nilsson *et al.* 1994; Andersson and Nilsson 2002; Boedeltje *et al.* 2003). During low river flow mainly local dispersal occurs, as there is not the energy in the river system for long distance transport.

The study found >2.5x more species were only in the lower Wingecarribee (sites 3 & 5) instream species pool in comparison to the upper site (site 1) or the tributaries. Similarly, there were significantly more non-native species in the main channel than in the tributaries, potentially dispersed down from the upper Wingecarribee River. This increase in species indicates a level of connectivity down the river system resulting in greater species richness, as hypothesised by the river accumulator hypothesis (Nilsson *et al.* 1991), although not shown directly from the instream sampling at low flow. Species specific to the headwaters can be dispersed down the river increasing the instream species pool's richness and abundance with distance down the channel. Alternatively, those species only found at the lower sites have little upstream dispersal capacity. Evidently, long distance dispersal through the catchment may be occurring accumulating a high variety of species in the lower catchment, but only at specific times such as during high flow events.

Dispersal through the catchment may mainly occur only during flood events, which is a period of high connectivity and long distance fluvial seed dispersal, such as hypothesised by the flood pulse concept (Junk *et al.* 1989). During high flow periods geomorphic features such as rocks and large woody-debris are overtopped reducing their seed trapping capacity (Nepf 1999). Whereas, flow fluctuation, the rate of the rise or fall of the flood pulse, was found to be the main influence causing seed deposition during high flow events (Merritt and Wohl 2002). During the main flood event (June 2007) species richness was 30% higher in the lower Wingecarribee River (site 5) and there was an increase in the proportion of species found only in the lower catchment in comparison to periods of lower stream flows; although these results should be taken with caution as the sampling protocol was not followed exactly because of lack of access and personal safety risk. Species accumulation may be occurring in a river system, but only for short periods within a flood event (Andersson and Nilsson 2002; Boedeltje *et al.* 2004; Vogt *et al.* 2004;

Hopfensperger and Baldwin 2009), and thus may not necessarily be identified through coarser temporal sampling methods. Therefore only local dispersal occurs at low flow, but long distance dispersal and species accumulation takes place possibly over a short period such as during the rising limb of the flood peak (Cellot *et al.* 1998) until seed exhaustion occurs. Connectivity down the Wingecarribee catchment did seem to be occurring as there were few species that were specific to the upper catchment or tributaries that were not found in the lower catchment. But the lack of samples and the varied and coarse sampling technique during the flood sampling only partially provide quantitative evidence for long distance dispersal within the Wingecarribee catchment.

Urban and agricultural areas are considered to be of lower species richness than those that are less disturbed (Hancock *et al.* 1996). However, it should be noted in the Wingecarribee catchment during low flow the two upper catchment sites (sites 1 & 2), which were more highly developed, had higher or comparable species richness and seed density and did not have significantly higher weed species in the instream species pool in contrast to their corresponding down stream sites (Figure 3.3). Medway Rivulet was the larger of the tributaries which may account for the relatively high species richness. Whereas, the upper Wingecarribee site (site 1) might reflect the upstream mixed land use of urban, agriculture, riparian vegetation rehabilitation and reserve land, and that many of the weeds have already been dispersed down the river.

3.5.3 Temporal variability in hydrochorous seed composition

Distinct seasonal changes in the fluvial seed rain was found, as previously shown in the Northern hemisphere studies (Cellot *et al.* 1998; Merritt and Wohl 2002; Boedeltje *et al.* 2004), with the main control to the instream species pool being seed release phenology of the local vegetation. This is shown by the distinct seasonal changes in the fluvial seed density and species richness in the river despite little increase in discharge (Figure 3.3). For example, in Joadja Creek during autumn (May 2008) discharge did not increase markedly from the previous month, but seed density doubled. Similar increases occurred at all sites on the Wingecarribee River despite minimal augmentation in river flow. The main channel showed stronger seasonal trends than the tributaries, as shown by groups four and five of the cluster analysis (Figure 3.4; Table 3.3), which were divided into seasonal subgroups (‘a’ and ‘b’). The more distinct seasonal changes in the main channel may be because of relatively high flows in the Wingecarribee River because of interbasin transfers of water

for urban consumption increasing the carrying capacity of the river. Conversely, drought lowered river flows in the tributaries during peak seed dispersal periods so seed were not so readily transported. The lack of distinct seasonal changes in seed density and species richness within the tributaries shows the importance of timed environmental flows for hydrochory and the potential reduction in river connectivity because of climate change reducing flow levels.

Along Black Bobs Creek seasonal variability was not so distinct. During the sampling period there was extensive river rehabilitation work upstream of the sampling site. The first site was moved as the result of this work. Even so, work upstream from the second site may have disturbed the soil seed bank and serotinous seeds during the winter and spring of 2007 causing the unseasonal results.

3.5.4 Water velocity influence on instream seed density and richness

Diaspore availability regulated fluvial seed rain within the Wingecarribee catchment. Distinct seasonal changes in fluvial seed composition coincided with the seed release period of riparian vegetation. However, the winter flood of 2007 caused a peak in seed numbers. Outliers from this peak skewed the relationship between water velocity and seed density (Table 3.5), resulting in a better fit than previously reported (Goodson *et al.* 2001; Boedeltje *et al.* 2003; Gurnell *et al.* 2007). However, by not taking the flood data into account, the regression coefficient between water velocity and seed density was weaker (R^2 = 0.1; P = <0.005). This weaker relationship was caused by a high density of *Casuarina cunninghamiana* and *Conyza bonariensis* seed, which made up >80% of total propagules. Therefore, a better model fit was calculated by removing these outliers (Table 3.5). The low correlation found in the Wingecarribee catchment between water velocity and seed composition at low river flow gives further evidence that the river was limited by the seed release timing of the riparian vegetation, while at higher flow seed may have been re-suspended from the substrate or transported long distances from upstream vegetation.

Temporarily stored seeds may be remobilised during low seed release periods. From early winter to late summer, disregarding the 2007 flood, >300 viable seeds of 33 species were collected in the Wingecarribee catchment (Figure 3.3). During these periods there was a stronger relationship between water velocity and seed density (R^2 >0.44; P = <0.005) than in autumn (R^2 = 0.16; P = 0.016), which had high seed release inputs (Table 3.5).

Similarly, during the flood in 2007, there was an increase in fluvially transported seed even though serotinous seed banks were low (Figure 3.3). The sources of these seeds, therefore, were most likely to have derived from soil or substrate seed banks along the channels (Nilsson *et al.* 1994).

Depletion of seed availability may have occurred within the Wingecarribee catchment during the flood. Seed density and species richness decreased substantially in the month after the flood. Similarly, comparing seedling germination results between consecutive August months in 2007 and 2008, the instream seed density of the latter was generally considerably higher. This seed depletion seems similar to that for suspended sediment depletion within a fluvial environment (Walling and Webb 1982).

3.5.5 Management implications

The large amount of native and non-native species moving though the catchment shows the importance of understanding the impact of fluvial seed rain within a catchment. The results of this study have implications for catchment managers, as well as for agriculturalists as major alien species such as *Nassella trichotoma* and *L. peploides* were found dispersing through the river system. For many species a high proportion of seed were collected only from one sampling site, such as for *L peploides*, indicating that it was mainly located in one region and if this area was targeted early for weed control extensive infestation may be averted. The large seed rain from *C. cunninghamiana* shows the potential of using fluvial dispersal as a means to facilitate rehabilitation of native riparian vegetation. To help understand and manage riverine seed rain better there is a need to identify the sources of the propagules. In this study it was shown that 30% of the seed collected was related to the phenology of seed abscission. The question arises, are the soil seed banks acting as an alternative source? The latter would explain the relatively high levels of fluvial seed rain that were observed during periods of out-of-season seed abscission. Increased knowledge of fluvial seed rain and its sources such as found by this study will improve understanding and potentially reduce costs of riparian vegetation management at the catchment scale.

3.6 Conclusion

Hydrochory is an important dispersal method for many species, as shown by 11 577 viable seed of 79 species that were collected from instream sampling throughout the Wingecarribee catchment over 17 months. To accurately quantify the instream species

pool, cross channel net position is important. Sampling in the highest water velocity stream line will capture the highest density of seeds, but a central position in the channel in relation to the banks will better represent all locally derived seed. This is particularly relevant when sampling on meanders or in a channel where the cross channel velocity profile is not evenly distributed.

Distinct spatio-temporal separation of the instream species pool was found within the catchment indicating that at low flow diaspores were locally derived with the main influence coming from the seed release phenology of the riparian vegetation. At higher flows potentially long-distance dispersal occurred and/or seeds were remobilised from the soil seed bank, which increased species richness and abundance within the river system. Although this study is limited in the timeframe of sampling, it shows the importance of environmental flows for dispersing native riparian species, such as *Casuarina cunninghamiana*, to connect up otherwise isolated patches of riparian vegetation. Alternatively, the potential detrimental impacts of lower flows caused by climate change resulting in reduced connectivity, lowered genetic diversity and decreased fitness in already isolated patches of riparian vegetation.

Chapter 4: The relationship between instream seed pool and three seed sources: soil seed bank, riparian vegetation and aerially dispersed seed

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Groves J.H., Williams D. G., Norris R. H., The relationship between instream seed pool and three sources: soil seed bank, riparian and aerially dispersed seed

4.1 Abstract

This chapter compares the species composition of three potential seed sources to the instream species pool at six sites in the Wingecarribee catchment, New South Wales, Australia. The instream species pool was sampled with floating traps and the aerial seed rain with bucket seed traps to measure the richness and abundance of seed that were entering the riparian zone, over 17 months. The standing riparian vegetation was surveyed and the soil seed bank sampled upstream from each sampling site to quantify the local seed sources. The seeds sampled from the instream species pool were also related to four life history traits: species origin, life cycle, vegetation type and seed float time, and the influence of water velocity on the number of non-local species in the instream species pool.

A total of 208 species were found from all survey and sampling methods, with 90% of the instream species pool accounted for by the local vegetation and seed banks, indicating that most species were locally derived. Cluster analysis of the species composition found a distinct separation between the survey/sampling methods with a secondary spatial separation delineating land use patterns. Along the Wingecarribee River there were seasonal shifts in the instream species pool seed source, controlled by relative seed availability from the standing vegetation. Whereas, life history traits identified did not indicate that a species may be more abundant in the instream species pool. High levels of non-native species found throughout all survey/sampling methods highlights the need for integrated alien species eradication programs that target not only the riparian zone but also upland vegetation and soil seed banks.

4.2 Introduction

River flow enables transport and exchange of matter, energy and biota between regions, generally described as a linear downstream path (Goodson *et al.* 2003; Boedeltje *et al.* 2004; Sannikov and Sannikova 2007), although lateral exchanges also occur (Junk *et al.* 1989). This capacity of rivers to transport material long distances, including propagules, means that a possible outcome is that plant species harnessing this form of dispersal may extend their range rapidly, which may in turn change the structure of downstream communities.

Previous research has focused on relating hydrochorous seed composition to the structure of the standing riparian vegetation. This relationship has been studied either through sampling instream propagules (Boedeltje *et al.* 2003), soil seed banks (Goodson *et al.* 2001), drift line material (Vogt *et al.* 2006), diaspore mimic dispersal (Andersson *et al.* 2000) or through riparian vegetation surveys (Jansson *et al.* 2005), all of which have shown positive relationships with local and upstream riparian vegetation.

Hydrochorous seed, however, may come from a variety of sources moving through multiple phases and by different vectors of transport. On a local scale, fluvial seed dispersal was shown to be a secondary vector of transport, with seed fall the primary vector; the water redistributed diaspores of *Taxodium distichum* (bald cypress) and *Nyssa aquatica* (water tupelo) to a more favourable position, although only short distances from their parent source (Schneider and Sharitz 1988). Long-distance fluvial dispersal may be one source of non-local hydrochorous propagules, with transport occurring mainly during periods of high flow (Nilsson *et al.* 1994). Alternatively, seed may be dispersed from upland vegetation into the river channel, in which case wind dispersal is the primary transport vector and hydrochory secondary (Renofalt *et al.* 2005). Seed found in the instream species pool may also be derived from local soil seed banks and substrate, where they have been previously deposited, temporarily stored and remobilised during high flow events (Andersson and Nilsson 2002; Gurnell *et al.* 2008). Propagules found in the instream species pool may originate from a variety of local and regional seed pools, but because of changing conditions and seed availability the dominant source of seeds may vary.

Hydrochorous seed sources may change seasonally (Andersson and Nilsson 2002; Boedeltje *et al.* 2004; Merritt and Wohl 2006). A species' peak period of seed release often coincides with local climatic and river flow regimes which both help to increase its dispersal and fecundity (Pettit and Froend 2001). For instance *Eucalyptus camaldulensis* seed release was shown to correspond with high stream flow events (Bren and Gibbs 1986). However, during periods of low seed release hydrochorous seed may be derived from other sources. Seasonal changes were shown to occur along the Cole River, UK; during summer the local floodplain was deemed to be the source of the propagules, whereas during winter upstream sources dominated the seed bank (Gurnell *et al.* 2006). The seasonal shifts in hydrochorous seed source, such as found along the Cole River, may

be relative to its availability from various sources. During high seed release periods the instream seed pool may be derived mainly from the local riparian vegetation, whereas during other periods, alternative seed sources may be represented more in the instream diaspore composition because of the lack of direct dispersal from the local plants.

All seed can disperse by water, but certain life history traits and seed morphologies are advantageous (Johansson and Nilsson 1993; Hancock *et al.* 1996; Naiman and Decamps 1997; Nilsson and Svedmark 2002). Different strategies are needed to optimise and endure hydrochory in different climates; tropical rivers have distinct annual monsoonal peaks, whereas temperate rivers often have variable flood histories (Pettit *et al.* 2001). During dispersal, seed can be subjected to extreme conditions, such as freezing, immersion and abrasion. These different conditions may either reduce seed viability or act as a trigger for germination. Diaspore morphology can impede or facilitate fluvial transport. Seed morphology that facilitates wind dispersal is also suited to hydrochory. Seeds that are either plumed (e.g. *Taraxacum officinale*) or winged (e.g. *Acer saccharum*) are also generally light and have a larger surface area, so they are more likely to float or be transported in the water column. Similarly, diaspores such as those from *Casuarina cunninghamiana* (river she-oak) have small wings (relative to embryo size) which limit flight, but aid their float time (Woolfrey and Ladd 2001). Therefore, plants use various life history strategies and traits, such as reproductive phenology, seed morphology, and float time to increase their dispersion and viability (Goodson *et al.* 2001).

This paper investigates the potential sources of diaspores to the instream seed pool and the transport vectors that move seed, and relates this information to species life history. Our study was applied at the catchment scale by quantifying the seed inputs from multiple sources of seed: either as aerial seed inputs (potentially from upland vegetation), or river bank soil seed banks, or those from local standing riparian vegetation. The particular questions that were addressed were: (1) How does the instream species pool differ from the three potential sources of seeds (standing riparian vegetation, soil seed bank and aerially dispersed seed), and is there any common spatial separation between river reaches? (2) Are there characteristic life history traits that cause the divisions between the different seed sources and dispersal vectors? (3) Does the instream seed pool contain relatively more non-local species as discharge increases? (4) Is there seasonal variation in the dominant source of instream seeds? Specifically, during autumn (the period of high seed abscission)

the composition of the instream seed pool is predicted to be closer to that of the standing riparian vegetation. Alternatively, during the rest of the year (periods of lower seed release) the composition of the instream seed will be closer to that of the soil seed bank.

4.3 Methods

4.3.1 Study site

The study was carried out at six sites in the Wingecarribee Catchment in southeastern Australia, which has an area of 763 km^2 (Figure 4.1). The catchment is divided between cleared farmland at the top of the catchment, and open *Eucalyptus* forest in the lower catchment. The average rainfall is 500 mm per year and the catchment has an average temperature range of 10 - 30^oC. The Wingecarribee River runs from the Wingecarribee reservoir at the headwater to the confluence of the Wollondilly River. At the beginning of the sampling program (2007) the region was in an extended drought. However, the Wingecarribee River is used for inter-basin transfers for Sydney's water supply, resulting in the flow regime being dictated by releases from the headwater dam (Figure 4.1). Therefore despite a period of drought, discharge was more consistent during the sampling period than in corresponding rivers (Table 4.1). The tributaries are unregulated creeks that are one quarter the size, and have an order of magnitude lower discharge, than that of the main channel (Table 4.1). Medway Rivulet passes through cleared farmland with minimal protection from stock. Joadja Creek and Black Bobs Creek are surrounded by open forests of *Eucalyptus, Acacia* and *Casuarina* species, and are fenced off or are not accessible to stock.

4.3.2 Instream sampling

Instream sampling and post-processing were carried out as described in Chapter 3. In brief, instream sampling was carried out from March 2007 once a month for 17 months at each site in the Wingecarribee catchment (Figure 4.1). Two nets were placed, one in the highest water velocity section of the river and the other in the centre of the channel for 5 hours at each site. The nets were positioned in the water so that 2/3 of the net was under water, thus sampling the top 10 cm of the river. Concurrent with the sampling, the stream dimensions and water velocity were measured or taken from a gauge station. The samples were taken

back to the laboratory, dried, Cold stratified at 4 ^{o}C (14 days), weighed and stored until they were prepared for germination.

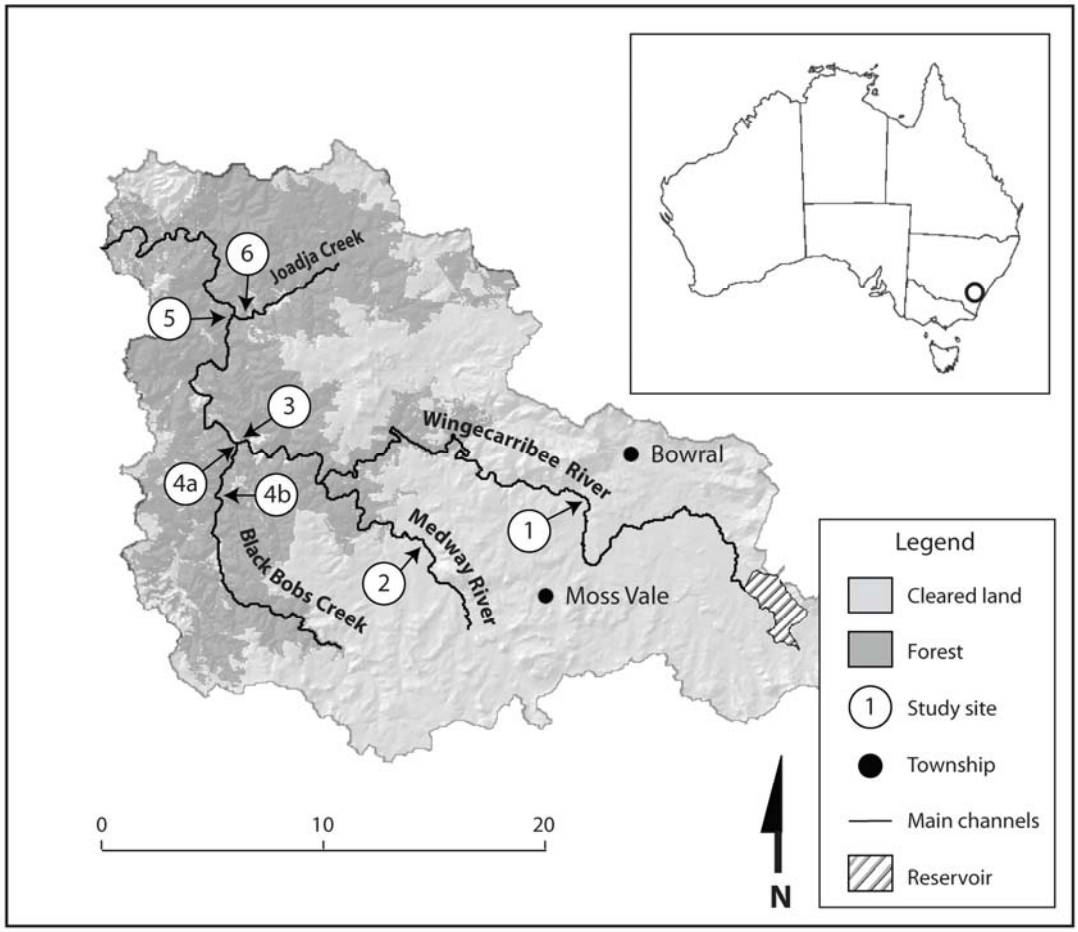

Figure 4.1 Location of study sites in the Wingecarribee catchment, New South Wales, Australia. The catchment is divided between cleared farmland at the top of the catchment, and open *Eucalyptus* forest in the lower catchment. The sampling site on Black Bobs Creek was originally 200 m upstream from the confluence with the Wingecarribee River (site 4a); however, because of upstream development and riparian rehabilitation works, the site was moved (July 2007) 5 km up the creek (site 4b)

4.3.3 Riparian zone soil seed bank

Soil core sampling was carried out in July 2007 at six randomly-chosen sites within 100 m upstream from each of the instream sampling sites, which encompassed or adjoined a section of river that had been surveyed for flora (Figure 4.1). At each soil core site, two subsamples with six aggregate random sediment cores of 5 cm depth and a diameter of 5 cm were collected from a quadrat of 1 m^2. A total of 72 soil samples were collected from

the Wingecarribee Catchment and taken back to the laboratory where they were air dried and stored until they were germinated.

Table 4.1 Average discharge, stream dimensions and site characteristics for each sampling site within the Wingecarribee catchment, New South Wales Australia (Figure 4.1)

Site	River	Average Discharge (m^3s^{-1})	catchment area (km^2)	Width (m)	Length (km)	Stream Order (Strahler)	Riparian cover‡
1	Wingecarribee River	5.30	205	20	80	2	Low
2	Medway Rivulet	0.08	93	4	17	4	Low
3	Wingecarribee River	5.30	431	20	80	6	High
4	Black Bobs Creek	0.05	125	3	18	*4	High
5	Wingecarribee River	5.30	598	20	80	6	High
6	Joadja Creek	0.20	104	6	8	4	High

*Originally located on a 5th order reach (Site 4a, Fig. 1), but because of upstream development and riparian rehabilitation work the site was moved (July 2007) 5km up the creek (Site 4b, Fig. 1)
‡Riparian cover: high >50%, low <50%

4.3.4 Germination trials

Germination trials were used to determine species richness and abundance of the collected instream and soil core samples. Sterilised sand was used as the base and an even layer of debris or soil was spread over 0.4 m^2 trays. The two instream samples from each site were mixed and then re-divided into two subsamples. One treatment was watered daily and the other was submerged under 5 cm of water (Brock *et al.* 1994). If the amount of debris that was collected was >1 L, a second tray was used. Alternatively, if the sample was <0.01 L only a watered treatment was germinated. Similarly, for the soil seed bank samples, one of each replicate was germinated in either a watered or a submerged treatment.

The samples were planted out in September 2007 and the consecutive year for the ongoing instream samples. They were removed the subsequent February. The glasshouse was watered for 15 minutes each day from an automatic system and maintained at 24°C during the summer by evaporative cooling. As seedlings emerged they were identified and removed, those species that were not identified at the end of the experiment were re-potted and grown until they flowered. Plants were identified using the Flora of NSW (Harden 1990 - 1993) and any further verification was carried out at the Australian National Herbarium, Commonwealth Scientific and Industrial Research Organisation (CSIRO) Plant Industry, Canberra.

4.3.5 Aerial seed

Aerial seed rain was measured with seed bucket traps immediately upstream from four of the sampling sites (sites 1 – 4) as described in detail in Chapter 3. Briefly, 10 seed bucket traps were placed directly upstream from the instream sampling sites, at random sites 50 m apart. They were emptied once a month to coincide with the instream sampling. Although they were attached to the ground with pegs, cattle, wombats and flooding occasionally knocked some of them over. A total of 657 samples were taken back to the laboratory and the number of seeds counted under a microscope. Identification of the seeds was done through germination trials, although only those diaspores that were represented by >10 for the whole 17 months of sampling were germinated. Germination was carried out as described above, although only a watered treatment was carried out, because taxonomic identification was required.

4.3.6 Riparian vegetation survey

Upstream from each instream sampling site the riparian vegetation was surveyed. Four plots replicated twice were randomly located up to 5 km upstream from each sampling site. Each site was located adjacent to the stream bank and consisted of two replicates 1200 m^2, 30 m wide. In the case of a road or escarpment the width was adjusted, but the area was kept constant. All standing vegetation within the survey area was recorded using the Braun-Blanquet classification method. Tree and shrub cover were recorded for the entire plot. Herbaceous vegetation was sub-sampled (1 m^2); 4 – 8 random plots were located within each survey area. The number of replicates depended on the variability in plant richness between sub-plots. Identification to species was done using the Flora of NSW (Harden 1990 - 1993) and any further verification was done at the Australian National Herbarium, CSIRO.

4.3.7 Vegetation life history traits

Life history characteristics: species origin: Native or exotic; life cycle: annual biennial or perennial; and vegetation type: graminoid, forb, shrub or tree, were derived from literature (Harden 1990 - 1993). Seed float time data were obtained through experimentation. Seed from 51 species were collected from the sampling sites throughout the Wingecarribee catchment during field work. A two month float time test was used to determine the floating capacity of the diaspores for each species. Three replicates of 50 seeds from each

species were floated in plastic containers (15 x 10 x 5 cm). The number of achenes that were still floating was recorded every 2 hours for the first 8 hours, then daily for two weeks and twice weekly for the remainder of the two months. The water in the trays was stirred vigorously and left for 10 minutes before each count. The percentage loss because of sinking was recorded for each time interval.

4.3.8 Data analysis

To describe the results of the vegetation survey and sampling, descriptive statistics were calculated. Variability in species richness and abundance between sampling sites were investigated using factorial analysis of variance (ANOVA) (SPSS 16). Seed density was $\log_{10}$ transformed to comply with the assumption of homogeneity of the variances.

To understand the separation between the sites within the catchment and sampling methods of the community structure, agglomerative hierarchical cluster analysis based on Sorensen's distance measure was calculated (PC-ORD 4). Eight samples from the instream sampling and 17 from the seed bucket sampling were removed from the analysis because the sampling period did not yield any seed. The data were relativized ($p = 1$) so that species abundance for each sample was proportional to the total value. The analysis categorised common assemblages between similarities in the species composition in relation to sampling method and spatial variability. The groups were identified by number and subgroups by letter and the percentage of sites that corresponded to each grouping was calculated. Plant species that indicated each group were identified by indicator species analysis.

Variability between life history traits in relation to the seed source or dispersal vector was calculated using factorial analysis of variance (ANOVA). To calculate the relationship between discharge and the number of non-local species, linear regression was used. Non-local species were defined by those species that were not found in the riparian vegetation survey upstream from each instream sampling site, therefore >5km upstream. The dependent variable was water velocity and the independent variable was the number of non-local species. Cooks distance was used to identify outliers, which were derived from the June 2007 flood and high autumn seed densities. All models were reported, both with and without outliers.

Seasonal changes to seed sources were calculated using ANOSIM (PRIMER 5), which evaluated the similarity within and between sites or sets of samples. An R value of one indicates total dissimilarity between the groups and zero indicates no dissimilarity; A *P*-value indicates significance of the dissimilarity..

4.4 Results

Overall 208 species were found from the riparian vegetation survey, soil core, instream sampling and seed bucket sampling, of which only eight were not able to be identified (Table 4.2). Of these identified species, 79 were found in the instream species pool, with 90% of those also present in the other survey and sampling methods (Table 4.3). Eight species were found in all surveys and sampling methods: *Casuarina cunninghamiana*, *Cirsium vulgare*, *Conyza bonariensis*, *Dactylis glomerata*, *Holcus lanatus* and *Hypochaeris radicata*. The instream species pool had 75% of the species in common with the local standing vegetation, 65% with the soil core samples and 60% with the aerial seed samples (Table 4.3). Eight species were found only in the instream pool (Table 4.2), all of which had low seed abundance and frequency (<1%), apart form *G. migrans* (2.35%) (Table 3.2).

The vegetation survey had >2x more species compared with the other sampling methods (Figure 4.2), with 54 species not found in the other seed pools (Table 4.3). The Wingecarribee River had 15% more species than its tributaries, but the only significant separation in species richness occurred between sites 2 and 4 with the other sites ($P < 0.001$, $F = 5.870$, df = 5, 42). The most common species that were found in the lower catchment but not at the two higher sites were: *Echium plantagineum*, *Casuarina cunninghamiana*, *Acacia parramattensis*, *Cyperus lucidus* and *Lomandra longifolia*, and at the head of the catchment but not at the lower sites were *Crataegus monogyna* and *Salix* spp.

Germination of soil core samples resulted in 80 species from 5 891 (SE 599) seed germinants (Figure 4.2). Of the soil core species, 15% were also found only in the instream species pool and seed bank (Table 4.3). There was no significant spatial separation between the six sample sites throughout the catchment for abundance ($P < 0.254$, $F = 1.351$, df = 5, 66) or richness ($P < 0.163$, $F = 1.634$, df = 5, 66). The most frequent and abundant species that were found in the soil seed bank were: *Conyza bonariensis,*

Gnaphalium americanum, Cyperus eragrostis, Isolepis inundata, Trifolium repens, Juncus articulatus, J. capitatus and *J. usitatus*.

The aerial seed had the lowest species richness in comparison to the results from other surveys and sampling methods (Figure 4.2), with 22 species and 5911 seeds captured over 17 months of sampling. Over 60% of the aerially dispersed species were also found in the instream species pool (Table 4.3). During peak dispersal, >1000 seed m^2d^{-1} where recorded, decreasing to zero during winter. There was no significant difference between the sampling sites for species richness ($P < 0.808$, $F = 0.324$, df = 3, 64) or abundance ($P < 0.409$, $F = 9.78$, df = 3, 64). Three species *Conyza bonariensis*, (site 2), *Digitaria sanguinalis* (site 2 & 3), and *Paspalum dilatatum* (site 3), were found in the seed buckets and instream species pool but were not found in the surrounding riparian vegetation, implying they may have dispersed from upland areas. The most common species that were aerially dispersing were: *Casuarina cunninghamiana, Paspalum dilatatum* and *Phalaris aquatica*.

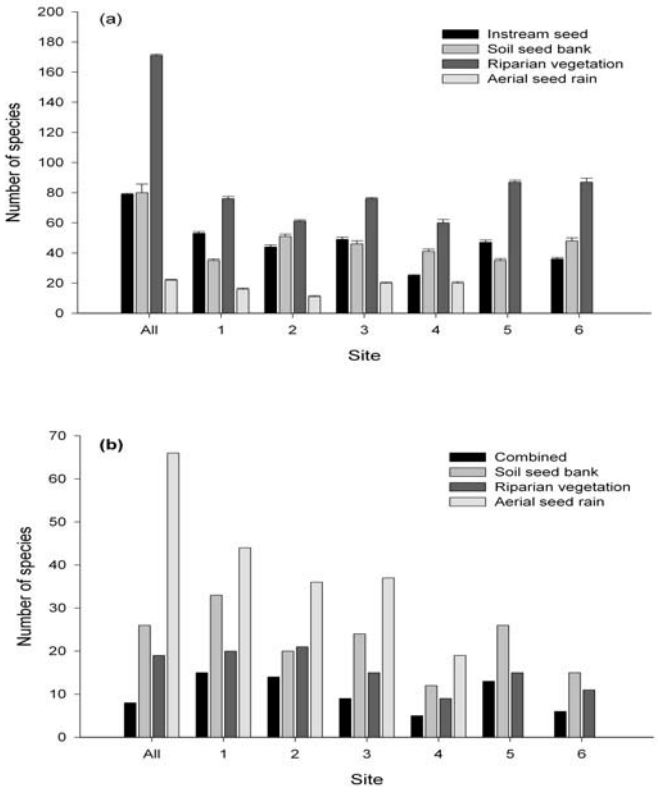

Figure 4.2 The total number of species that were found in each survey/sampling method in relation to the instream species pool (a) total species richness (b) number of species not found in the instream species pool

Table 4.2 List of species collected in aquatic seed traps over 17 months, and their occurrence in the soil seed bank, standing riparian vegetation, and aerial seed rain, from six sampling sites in the Wingecarribee catchment, southeastern Australia

Instream species	Species occurrence in		
	Soil	Standing vegetation	Aerial seed rain
Adiantum aethiopicum		x	
*Anagallis arvensis**	x	x	
*Anthoxanthum odoratum**		x	
*Bidens bipinnata**		x	
*Bromus catharticus**	x	x	
*Bromus hordeaceus**	x		
Cardimine paucijuga		x	
*Carduus tenuiflorus**	x	x	
Casuarina cunninghamiana	x	x	x
Centipeda minima			
Cerastium glomeratum	x	x	
*Chamaesyce maculata**		x	
*Chenopodium ambrosioides**	x		
*Chenopodium pumilio**	x	x	
*Cirsium vulgare**	x	x	x
*Conyza albida**		x	
*Conyza australis**			
*Conyza bilbaoana**		x	
*Conyza bonariensis**	x	x	x
*Conyza canadensis**		x	x
*Cynodon dactylon**	x	x	
Cyperus difformis	x	x	
*Cyperus eragrostis**	x	x	
Cyperus lucidus	x	x	
Cyperus sphaeroideus	x		
*Dactylis glomerata**	x	x	x
Dichondra repens	x	x	
Digitaria sanguinalis	x		x
Einadia nutans ssp. *nutans*	x	x	
Eleocharis sphacelata	x	x	
*Eragrostis curvula**		x	
*Fumaria muralis**	x	x	
Galium migrans			
Geranium solanderi	x	x	
*Gnaphalium americanum**	x		
*Hirschfeldia incana**		x	
*Holcus lanatus**	x	x	x
Hypericum japonicum	x		
*Hypochaeris radicata**	x	x	x
Isolepis inundata	x	x	
*Juncus articulatus**	x	x	
*Juncus capitatus**	x		
Juncus usitatus	x		
*Lactuca sativa**		x	
*Lactuca serriola **		x	

Table 4.2 (continued)

Instream species	Species occurrence in		
	Soil	Vegetation survey	Aerial seed rain
*Lolium perenne**	x		
Lomandra fluviatilis		x	
Lomandra longifolia		x	
Ludwigia peploides	x	x	
Lycopus australis	x	x	
Microlaena stipoides	x	x	
*Modiola caroliniana**	x	x	
*Nassella trichotoma**		x	
*Oxalis corniculata**	x	x	
Oxalis perennans	x	x	
*Oxalis pes-caprae**	x		
*Paspalum dilatum**	x	x	x
*Persicaria maculosa**			
Persicaria hydropiper	x	x	x
Persicaria prostrata			
Phragmites australis	x	x	
*Plantago lanceolata**	x	x	
Poa labillardieri	x	x	
*Poa pratense**	x	x	
*Polycarpon tetraphyllum**			
*Pontederia cordata**	x		
Pratia purpurescens			
*Romulea rosea**	x	x	
*Rorippa palustris**	x	x	
*Rubus fruiticosus**		x	
*Rumex conglomeratus**		x	
*Rumex crispus**	x	x	x
*Rumex obtusifolius**		x	
*Rumex brownii**	x	x	x
*Scirpus polystachus**			
*Solanum nigrum**	x	x	x
*Sonchus asper **	x	x	
*Trifolium repens**	x	x	
*Verbena bonariensis**	x	x	

*Non-native species to Australia

Table 4.3 The number of species, and standard error (SE), found in the instream species pool, soil seed bank, standing riparian vegetation, and aerial seed rain at six sampling sites in the Wingecarribee catchment; also presented are the number of species that are in common, or not, between the instream species pool and the survey or sampling methods

Variable	Sample site						
	Catchment	1	2	3	4	5	6
Total number of species found in river	79	53	44	49	25	47	36
SE	0.60	1.21	1.41	1.61	0.57	1.52	0.99
average number of seed (m^3/s)	0.243	0.163	0.359	0.001	0.001	0.004	0.371
SE	0.1445	0.0563	0.2596	0.0004	0.0003	0.0023	0.1470
Total No. of species present in soil core	80	35	51	46	41	35	48
SE	5.75	1.02	1.50	2.10	1.60	1.23	2.01
Total No. of species present in the soil seed bank and the instream species pool	53	20	24	25	13	21	21
Total No. of species present in the soil seed bank, but not the instream species pool	27	15	27	21	28	14	27
Total No. of species present instream, but not in the soil seed bank	26	33	20	24	12	26	15
Total No. of species present in riparian vegetation	171	76	61	76	60	87	87
SE	0.84	1.45	1.05	0.76	2.15	1.18	2.62
Total No. of species present in the riparian vegetation and the instream species pool	60	33	23	34	16	31	25
Total No. of species present in the riparian vegetation, but not the instream species pool	111	43	38	42	44	56	62
Total No. of species present instream, but not in riparian vegetation	19	20	21	15	9	15	11
Total No. of species present in the aerial seed rain	22	16	11	20	20		
SE	0.37	0.67	0.71	0.68	0.92		
Total No. of species present in the aerial seed rain and the instream species pool	13	9	8	12	6	0	0
Total No. of species present in the aerial seed rain, but not the instream species pool	9	7	3	8	14	0	0
Total No. of species present instream, but not in the aerial seed rain	66	44	36	37	19		
Total No. of species present instream, but not found in any survey	8	15	14	9	5	13	6

4.4.1 Variation between seed sources and instream seed pool

Species composition data derived from all four surveys were grouped through the use of cluster analysis, based on the Sorensen similarity index (Figure 4.3). The cluster groups are referenced by number, which show distinct separation between the sampling methods (Figure 4.3; Table 4.4). Groups two and four from the cluster analysis show nearly complete alignment with standing vegetation and the soil seed bank respectively (Table 4.4). Group three is composed of the aerial seed rain (70%) and by the instream seed trap samples (30%). The instream seed samples in this group were mainly sampled during the peak seed dispersal period (February to June). Group one represents the instream species pool, with some influence from both the soil seed bank and from aerially dispersed seed (Table 4.4). The instream samples that show most alignment with the soil core samples, in group one, are those samples that were taken during periods of low seed release (July to January) or during the flood (June 2007). The groups were further subdivided into subsets, indicated by letters, which show distinct spatial alignment between the upper and lower catchments (Figure 4.3; Table 4.4). The standing riparian vegetation shows the most distinct alignment, with only subgroups ‘e’ and ‘g’ not well grouped spatially.

4.4.2 Life history

The Wingecarribee riparian zone was dominated by exotic species (>60%), which were found in all survey/sampling methods (Figure 4.4). A greater representation of native species was found in the standing riparian vegetation, but there was no significant difference between the survey/sampling methods ($P < 0.808$, $F = 0.052$, df = 2, 174). Perennials were the most common species found within the catchment comprising >60% of the total species, with the soil seed bank having more annuals than the other surveys/samples. However, there was no significant difference between the survey/sampling methods in the life span of the species ($P < 0.515$, $F = 0.666$, df = 2, 174). The most common life form was forbs comprising 50% of species dispersing through the catchment. Tree and shrub species richness of the standing vegetation and aerial seed rain was significantly higher ($P < 0.037$, $F = 3.350$, df = 2, 174) than that found in the instream species pool and seed bank.

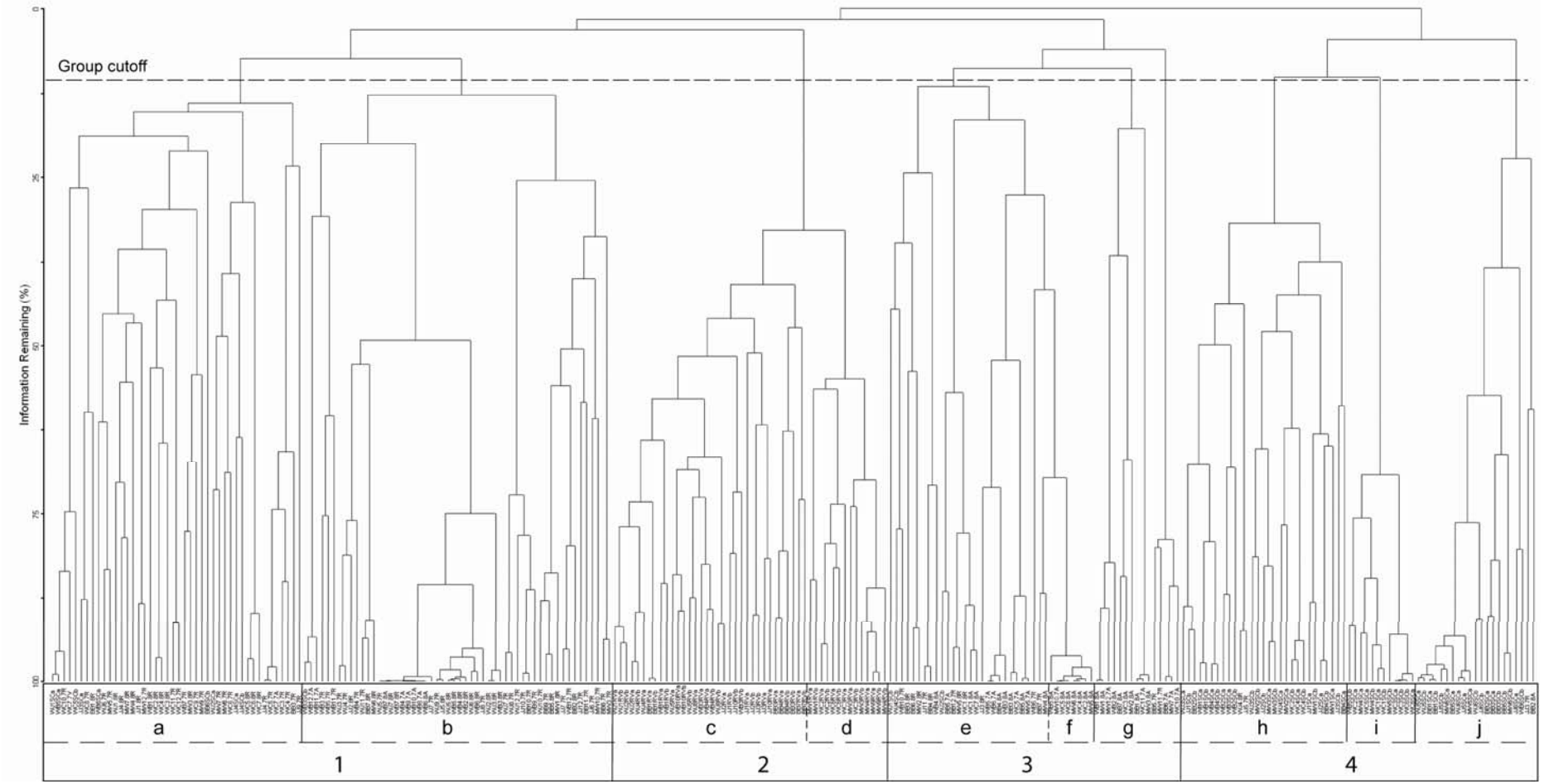

Figure 4.3 Cluster dendrogram of species composition of instream species pool, standing riparian vegetation, aerial seed rain and soil seed bank from six sampling sites within the Wingecarribee catchment, Australia, the main groups are represented by number 1 – 4, and subgroups are represented by letters a – j, the interpretation of the groups and subgroups are presented in Table 4.4, lines represent major and dotted lines represent minor separation between groups

Table 4.4 Groups and subgroups showing separation between the survey methods (groups 1 – 4), and spatial division between the upper catchment and lower catchment (subgroups a – j), derived from the cluster analysis of species composition (Figure 4.3); presented is the proportion of each group, 'upper' and 'lower' are the spatial division for each group

Sampling source	catchment position	Groups and subgroups (%)									
		1		2		3			4		
		a	b	c	d	e	f	g	h	i	j
Number per group		44	54	34	14	28	8	15	29	12	21
Instream species pool	Upper*	55	7			11		20			
	Lower*	23	76			32		20	7		5
Riparian vegetation	Upper*				100						
	Lower*			100							
Seed rain[§]	Upper*	2				18	88	40			
	Lower*		15			29	13	20			5
Soil bank	Upper*	2							31	92	14
	Lower*	18	2			11			62	8	76

*Upper catchment represents sites 1 and 2; the lower catchment represents by sites 3 – 6 (Figure 4.1)
[§]Samples were only collected from sites 3 – 6

4.4.3 Abundance of non-local species in relation to water discharge

On average 6.9 (SE 1.3) non-local species were collected from the instream species pool at each sampling site. The upper Wingecarribee River (site 1) had the most non-local species. A weak significant relationship was calculated between water velocity and the number of non-local species (Table 4.5). A stronger correlation was found when the results of sampling of the species during the flood were included, most notably shown by the 50% increase in the model fit for the winter period (Table 4.5).

Table 4.5 Relationship between water velocity and the number of non-local species at six sites within the Wingecarribee catchment, New South Wales, Australia; summarised are the regression models for all samples, also shown are models excluding outliers caused by a flood event (June 2007); the results presented are the model fit and significance levels

	All sampling				No Flood			
	R^2	df	F	P	R^2	df	F	P
All sites together	0.143	1,99	16.516	<0.005	0.104	1,94	10.953	0.001
Individual sites								
Summer	0.141	1,16	2.629	0.124				
Autumn	0.157	1,34	6.331	0.017				
Winter	0.365	1,27	15.53	0.001	0.232	1,22	6.639	0.017
Spring	0.270	1,16	1.257	0.275				

4.4.4 Seasonal variation of instream seed composition

Instream species pool composition became more similar to that of the standing vegetation during the season of high seed release (autumn) (Table 4.6). Alternatively, along the Wingecarribee River (Sites 1, 3 and 5) increased in relation to the soil core samples during seasons of low seed release (winter to summer). However, the three tributaries did not generally reflect this gradient.

Table 4.6 Seasonal variation between the instream species composition with the riparian standing vegetation and soil seed bank (ANOSIM), where the lower the value the greater the similarity

Component		Site					
	Combined	1	2	3	4	5	6
Vegetation - Summer	0.788	0.870	0.886	0.941	0.901	0.902	0.949
Vegetation - Autumn	0.606	0.606	0.709	0.908	0.734	0.477	0.950
Vegetation - Winter	0.704	0.901	0.796	0.813	0.734	0.839	0.919
Vegetation - Spring	0.811	0.864	0.884	0.833	0.973	0.864	1.000
Soil core - Summer	0.579	0.721	0.847	ns	0.801	0.669	0.554
Soil core - Autumn	0.613	0.872	0.615	0.306	0.692	0.801	0.727
Soil core - Winter	0.543	0.784	0.703	0.297	0.734	0.765	0.618
Soil core - Spring	0.572	0.752	0.838	ns	0.615	0.737	0.636

ns: not significant

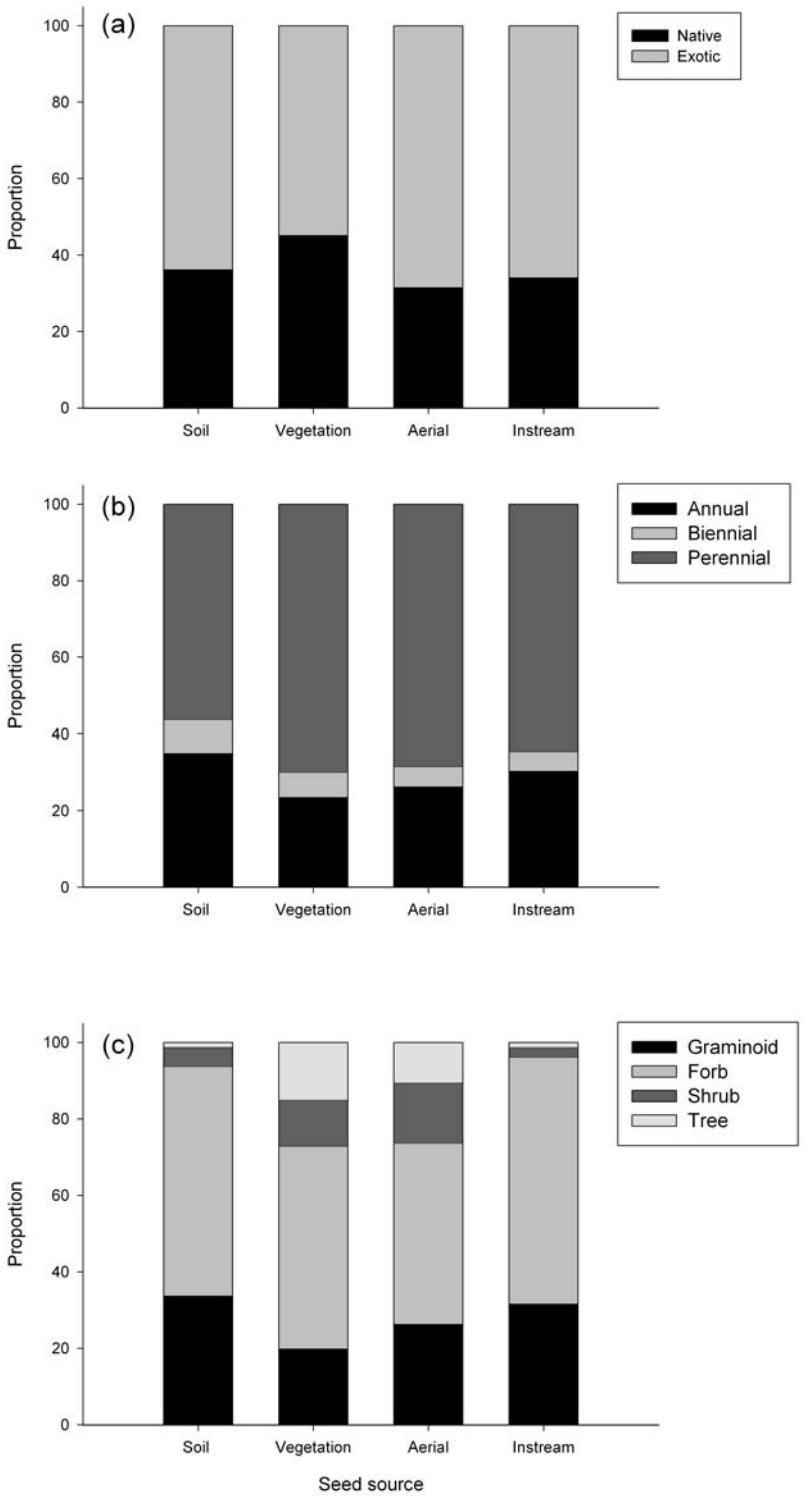

Figure 4.4 The difference in species number of three life history traits between four survey methods (a) species origin (b) life cycle length (c) vegetation type; soil seed bank, standing riparian vegetation, aerial seed rain, and instream species pool

4.5 Discussion

4.5.1 Variability between the local seed pools and the standing riparian vegetation

In regard to our first question, the cluster analysis showed distinct alignment between the instream species pool and the three potential seed sources/transport vectors (Figure 4.3; Table 4.4), thereby showing that seed dispersal into a region and the resulting vegetation structure has multiple inputs and influences. Results of the cluster analysis show that the standing riparian vegetation (group 2) had the most influence in determining the composition of the instream species pool, and secondly, the aerial seed rain (group 3) and thirdly, the soil seed bank (group 4) (Figure 4.3). The separation between aerial seed rain, the standing riparian vegetation and instream species pool may be because of the seasonality of the inputs (Chapter 3) and that some of the seeds may have dispersed from upland areas. The soil seed bank was most dissimilar to the instream species pool, which may be because only certain conditions such as high flow regimes were able to mobilise these seeds (Boedeltje *et al.* 2004; Gurnell *et al.* 2007).

Most species were locally dispersed. A total of 75% of the instream species pool was also present within the local standing riparian vegetation, which is similar to findings in the northern hemisphere (Schneider and Sharitz 1988; Middleton 2000; Boedeltje *et al.* 2003). Taking into account the aerially dispersed seed and soil seed bank, 90% of the species were found locally. Additionally, the subgroups derived from the cluster analysis separated the groups spatially between the upper and lower catchment, which reflects the land use divisions within the catchment (Figure 4.1). These results are consistant with the previous detailed analysis of the spatial distribution of the instream species pool (Chapter 3), the dispersal kernel of released mimics (Johansson and Nilsson 1993; Andersson and Nilsson 2002; Vogt *et al.* 2006). However, within the local vegetation and seed banks, 10% of the species were unaccounted for.

The instream species that were not found in the other survey/sampling methods potentially may have dispersed long distances through the river system (Table 4.2). The frequency and abundance of these species in the instream species pool were low (Chapter 3), implying that they may be outliers that dispersed >5km downstream from the instream sampling point, and thus outside the sampling area of the other surveys; an example is *Conyza*

australis which was represented by only seven seed trapped from one site (site 2) over 17 months of sampling, although it can potentially release hundreds of seed in a season. In comparison, its congener *C. bonariensis* was found profusely throughout the lower catchment's riparian zone and within the instream seed pool (Chapter 3). Similarly, soil seed banks (Goodson *et al.* 2002), litter deposits (Jansson *et al.* 2005) and instream samples (Nilsson *et al.* 1994) all had a portion of non-local species, which may potentially have dispersed long distances from the upper catchment. However it must be noted that sampling error of the potential sources of seed may also account for a portion of the instream species not found locally. Long distance dispersal may occur over a short period, such as during a flood peak (Andersson and Nilsson 2002), or through multiple stages of seed storage and remobilisation (Gurnell *et al.* 2008).

4.5.2 Multiple seed sources and dispersal vectors

The seed found in the instream species pool were derived from multiple sources and moved to the stream by various dispersal vectors. Anemochory (wind dispersal) can transport seed into and within a riparian habitat. A total of 36% of the species found in the aerial seed rain were not accounted for in the local vegetation. Furthermore, three species were found only from the aerial seed rain and instream species pool, at two sites, indicating that they were dispersed from outside the immediate riparian zone, coming presumably from upland vegetation, such as has been previously reported (Boedeltje *et al.* 2003; Renofalt *et al.* 2005). Soil seed banks can also act as a temporary store for seed that are moving through a catchment (Gurnell *et al.* 2007). The soil seed bank in the Wingecarribee catchment had 15% of the instream species that were not found in the standing vegetation or in seed buckets (Figure 4.3), indicating that these species were possibly dispersed from the upstream species pool. These species may be transported, deposited and remobilised several times as they disperse through the catchment (Gurnell 2007). A high proportion of the instream species pool was accounted for by the local vegetation, but 25% of the species caught fluvially dispersing did so directly through aerial or fluvial dispersal. Upon entering a reach they may germinate (or die) where they have been deposited or they may stay in the soil seed bank until they are remobilised and transported further through the catchment to a site more favourable for germination.

4.5.3 Influence of life history traits

All species are able to fluvially disperse; they just need the required stream power to transport their propagules. There was no significant difference in several life history traits that denoted a species would be found in the instream species pool (Figure 4.4), as has been previously found for similar life history traits (Merritt and Wohl 2006) and floating ability (Andersson *et al.* 2000). This result signifies that the life history traits that were analysed are not necessarily indicative of hydrochory, with many riparian species potentially being able to be dispersed fluvially because of their geographic proximity to the river channel. Primary dispersal may occur through aerial or gravitational vectors directly into the channel or into the riparian zone seed bank where diaspores may be mobilised by the river flow. Once in the water column, buoyant seed may be transported in the upper section of the water column, but negatively buoyant species may be transported either along with other floating organic mater (Jansson *et al.* 2005), saltate along the bed or be held in a temporary store in the substrate and remobilised during high flow periods (Gurnell *et al.* 2007). Many dedicated and other riparian species may therefore prefer riparian zones for other environmental reasons, such as the higher water table and soil fertility, than the potential to disperse fluvially. However, hydrochory is of benefit to plant species growing in riparian habitats, which enables long distance dispersal through the fluvial landscape.

Most notably seed float time did not influence species occurrence in the instream species pool, a particularly interesting result because the samples were taken from the top 0.1 m of the channel's water column. Previously, the relationship between seed float time and species occurrence in the environment has resulted in contradictory conclusions being drawn, with some researchers finding positive relationships (Johansson *et al.* 1996; Jansson *et al.* 2000; Andersson and Nilsson 2002), and others no relationship (Andersson *et al.* 2000; Jansson *et al.* 2000; Nilsson and Svedmark 2002; Gurnell 2007; Markwith and Leigh 2008). Since 90% of the species that were sampled were accounted for by local sources, they may not have been fluvially transported for a very long period, or may have deposited into temporary storage. There is increasing evidence that many non-aquatic species can survive temporary storage in the substrate seed bank (Gurnell *et al.* 2007); hence the ability to float for more than 24 hours does not seem particularly necessary for the dispersal of such species.

Species occurrence in the riparian environment was more important than life history traits for its presence in the instream species pool. Species such as *Rumex brownii*, which was abundant in the river, was also found extensively in samples using all survey/sampling methods, including the seed buckets, even though it does not have a particular morphology for aerial dispersal. Similarly, *Casuarina cunninghamiana* was found to be a common species in the lower catchment's riparian zone and was found extensively in the instream species pool and aerial seed rain. It also had a few germinants that were derived from the soil seed bank. The germinants of *C. cunninghamiana* derived from the soil seed bank most likely occurred because they had been recently released from parent trees at the time of collection. Species abundance in the riparian zone and thus its ability to release proportionally more seed than other species may be more important for the high occurrence in the instream species pool than other factors, because rivers are often seed-limited (Xiong *et al.* 2003). However, the presence of a species' propagules in a river does not necessarily mean that it will germinate downstream, but its presence will increase its chance of having a higher recruitment than that of another species.

There was a large proportion of non-native species in all survey/sample methods throughout the Wingecarribee catchment, indicating that these species were extensively established throughout the catchment and were dispersing from different habitats, both upland and riparian (Figure 4.4). Therefore, their seeds had an opportunity to deposit to a wide range of sites throughout the catchment enhancing the likelihood that a proportion of seed would reach suitable germination sites (Janzen 1970; Connell 1971; van der Valk 1981).The proportion of native to non-native species was higher than has been found in North America (Merritt and Wohl 2006). This difference may be because many of the species have been introduced from Europe and North America for grazing or urban plantings and the close proximity of these potential sources of seed to the Wingecarribee River. The high level of exotic species in the lower catchment indicates long distance dispersal potentially from the top of the catchment where there is more farm development and more urban area. The larger exotic species such as trees of *Acer pseudoplanatus* found in the riparian zone along Joadja Creek (site 6) were most likely derived from an abandoned colonial township 4 km upstream from the sampling point (personal observations). The extensive occurrence of alien species throughout all dispersal vectors and seed banks means any management of a species requires an eradication program that targets not only the riparian zone but also upland vegetation and soil seed banks.

4.5.4 Seasonal variation of instream seed composition

Seasonal changes to the instream species richness and abundance in the Wingecarribee catchment were found to be related to seed release phenology, with most seed dispersing during autumn (Chapter 3) also see (Dalling *et al.* 1998; Boedeltje *et al.* 2003; Boedeltje *et al.* 2004). During autumn, the period of high release, the instream species pool was most similar to that of the local riparian vegetation (Table 4.6). During the other seasons (winter to summer) the instream species pool became less similar to the riparian vegetation composition, and became more similar to that of the soil seed bank. Further, 10% of the samples in group 1 (instream species pool samples) were from the soil seed bank (Table 4.4). The instream samples that were most similar to the soil seed bank samples found in group 1 were those from the periods of low seed release or of floods (June 2007) (Figure 4.4), indicating that the soil seed bank was the dominant source of seed at these times in comparison to the riparian vegetation or to the aerially dispersed seed. Similar seasonal shifts were found along the Dove River, UK (Gurnell *et al.* 2006). Therefore, the local standing vegetation potentially contributes the most seed to the instream species pool during high seed release periods, whereas during other periods, the proportional input from other sources, such as that from the soil seed bank, may become more dominant.

4.5.5 Abundance of non-local species in relation to water discharge

As water velocity increases, seed were potentially transported further, and more non-local species were transported into a reach. There was a 60% difference in the model fit between the regression model which took the winter flood (June 2007) into account and the model which did not, showing the strong influence of water velocity on long distance transport. Flow separation, eddy formation and hydraulic complexity may cause some increase in seed retention at particular reaches (Merritt and Wohl 2002). However, water velocity has been shown to be a major factor in controlling the distance hydrochorous seed may be transported (Andersson *et al.* 2000; Riis and Sand-Jensen 2006). Higher water velocity facilitates the augmentation of shear stress and fewer dead zones resulting in longer dispersal distance and thus potentially more non-local species being directly transported into a reach from the upstream species pool (Groves *et al.* 2009) or else remobilised from the channel substrate (Gurnell 2007).

Large increases in water velocity and/or seed supply are needed to significantly augment the amount of non-local seed that is dispersed into a reach. During spring and summer

there was no significant relationship between river flow and non-local species (Table 4.5), which was probably because seed availability was limited and thus significant increases in seed abundance did not occur in line with the river flow fluctuations. However, during autumn high seed availability meant that there were more seed being deposited into the channel and thus a better chance for some outliers being able to disperse long distances through the catchment. Similarly, winter was influenced by the flood, and relatively high seed availability (Chapter 3). Water velocity is the major factor in seed dispersal, with larger flow fluctuations needed to mobilise seed during times when seed availability from the riparian vegetation is low.

There was a distinct separation of the species composition between the survey and sampling methods within the Wingecarribee catchment with a secondary spatial separation delineating land use patterns. Of the instream diaspores 90% were accounted for by local seed sources, with standing riparian vegetation being the dominant source. However, there was no indicative life history trait that denoted a species would disperse fluvially, thereby indicating that geographic proximity and chance were the main reasons for hydrochory. Therefore, all species can be dispersed fluvially, with water velocity the main factor controlling the mobilisation and distance a species may disperse, as indicated by the positive relationship found in this study between the number of non-local species and river discharge. However, seeds need to be available for transport. The standing riparian vegetation was most influential in determining the composition of the instream species pool during autumn (the period of high seed release). However, during the other seasons the soil seed bank became more similar to the instream species pool, thereby indicating seed availability to be the main control of seed abundance and richness within the Wingecarribee River.

Chapter 5: Fluvial seed dispersal and factors that influence deposition and potential loss

This manuscript is ready for submission to the journal 'Freshwater Biology'

Groves J.H., Norris R. H., Williams D. G., Fluvial seed dispersal, and factors that influence deposition and potential loss

5.1 Summary

1. Seed rain can be important in structuring riparian vegetation, with both alien and native species being dispersed fluvially.

2. It is important to quantify movement of the seed rain through the riverine environment to better understand riparian vegetation structure and its management.

3. To examine fluvial seed dispersal the dispersal kernel of *Helianthus annuus* (sunflower) achenes was quantified after 24 hrs, from time of release, along the Wingecarribee River and two of its tributaries, in southeastern Australia. Concurrently, the stranding pattern of the achenes was related to abiotic and biotic factors that may influence their aggregation and species abundance along the channel banks, while also taking into account seed loss from waterlogging and predation.

4. Over 50% of the achenes were deposited within 1000 m and 100 m from the point of release on the Wingecarribee River and its two tributaries respectively, with the furthest being transported 4500 m.

5. At the reach scale (>100 m), water velocity was found to be a significant predictor of the dispersal kernel. At the sub-reach scale (<100 m), all abiotic and biotic variables deemed to influence seed deposition were found to be significant, but were highly variable in causing seed aggregation, with the exception of pool/riffle sequences which consistently indicated that lower water velocity river section increase deposition.

6. The results of the experiments showed that: (a) even at low flow a few outliers can still potentially disperse >15x further than majority of the seed cohort; (b) water velocity is the main factor in determining the dispersal curve of fluvially dispersed seed both at the reach and sub-reach scale; (c) at the reach scale abiotic and biotic factors influenced seed deposition, but at the sub-reach scale there was high variability in their effect; and d) predation and sinking of fluvially dispersed seed potentially cause >65% of seed loss during the primary phase of fluvial dispersal.

5.2 Introduction

A range of dispersal modes are used by plants to extend their range and to maximise their recruitment, with outliers often being transported many kilometres from their parent source (Andersson *et al.* 2000). Even if diaspores are not transported to these distances, dispersal may facilitate recruitment by moving seeds to beneficial germination environments, reducing intra-specific competition and diminishing predation (Vander Wall and Longland 2004). Hydrochory, dispersal by water, is thus a potent process influencing plant distribution and abundance along rivers (Andersson *et al.* 2000).

Seed dispersal is multifaceted with diaspores often moving by multiple dispersal vectors and phases (diplochory) (Vander Wall and Longland 2004). In a riverine context, seeds may be deposited into the river through aerial, ballistic, animal or other primary dispersal methods, and then transported further by water. Once in a river, they may move through multiple periods of transport and storage until they germinate or lose viability (Gurnell *et al.* 2007). Over a five week experiment on the Vindel River in Sweden, Andersson *et al*. (2000) found that seed mimics were transported up to 55 km from their release point. At this temporal scale, seeds have potentially moved through multiple phases of transport and deposition (Gurnell *et al.* 2007; Markwith and Leigh 2008). However, there have apparently been no studies that investigate a single stage of diaspore transport over a short period (24 hours). During such a short period, the fundamental factors that influence diaspore transport and deposition can be investigated, because there is no significant temporal variation in flow.

The main factors found to influence fluvial seed dispersal are water velocity and river channel dimensions, although other environmental factors such as large woody debris, sinuosity and substrate, may also affect seed transport (Schneider and Sharitz 1988; Johansson and Nilsson 1993; Andersson *et al.* 2000; Merritt and Wohl 2002). Water velocity was established to be the main factor that caused seed deposition both in a laboratory flume (Merritt and Wohl 2002) and in a riverine environment (Andersson *et al.* 2000). Similarly, Riis and Sand-Jensen (2006), through propagule release experimentation, found higher water velocity and larger channels to be the main factors that influenced vegetative propagule dispersal. However, hydraulics and geomorphic features may influence deposition at different times in a flow regime. At high flow, hydraulics has been shown to influence seed deposition through recirculation in eddies or deposition in slack

waters and flow expansions (Merritt and Wohl 2002). Whereas, at low flow hydrologic energy is dissipated and geomorphic features become more exposed resulting in greater seed aggregation on these features (Merritt and Wohl 2002).

Many species have propagules that are capable of being transported by water (Boedeltje *et al.* 2004; Merritt and Wohl 2006). Fluvial dispersal of plant fragments is an important part of some species' dispersal strategy, such as *Ranunculus peltatus* (Pond water-crowfoot) (Riis and Sand-Jensen 2006). However, a larger variety of species disperse diaspores fluvially (Andersson and Nilsson 2002; Vogt *et al.* 2004). Instream seed samples from the Krvcklan River, Sweden, showed that over 80% of the species' reproductive material that were identified as diaspores, with only 20% being vegetative fractions (Andersson and Nilsson 2002). Therefore, the knowledge derived from understanding fluvial seed dispersal can be more broadly used and has implications for riparian zone management and rehabilitation.

Many river systems are highly disturbed because of development, resulting in remnant patches of native vegetation and increased openings for invasive species to establish. The distribution and rapid expansion of alien species along rivers is a visual reminder of how fast species can disperse. Outliers can potentially extend the range of alien species and connect up otherwise-isolated pockets of native riparian vegetation. Close to the parent source, there is higher intra-specific competition from both the adult plant and other seedlings from the same cohort (Howe and Smallwood 1982). Predation near the parent plant is similarly higher (Janzen 1971; Cavers 1983; Hulme 1998). Recruitment is therefore potentially greater for species that are able to disperse their propagules outside the parental sphere of influence, as described by the Janzen-Connell (J–C) pattern (Janzen 1970; Connell 1971).

Many riparian plants in temperate regions are serotinous, because flood events are unpredictable (Pettit and Froend 2001). In these regions vegetation relies on the river flow at the time of release to disperse. River regulation, extraction and channelisation all change the flow regime of a river, thereby impacting the dispersal of hydrochorous species. Increased drought frequency and/or climate change, such as have occurred in southeastern Australia over the last 12 years, have decreased the current flow levels, also potentially influencing fluvial dispersal patterns. An enhanced understanding of the implication of

lower flows on the sustainability of native species is needed for establishing the long-term viability of many riparian species.

In this paper, the potential complexities of multi-stage seed dispersal have been excluded by investigating hydrochory over a short period of transport. Our aim was to focus on the key parameters of hydrochory, the flow regime and channel roughness, to understand a single dispersal cycle by comparing the dispersal kernel of fluvially dispersed diaspores between differing flow regimes, while at the same time taking into account other potential factors that may cause seed to aggregate. Additionally, to understand the potential loss of seed in the environment and the impact of seed rain on the riparian vegetation structure. Specifically, our research questions were: (1) What is the dispersal kernel of fluvially dispersed seed over a short transport period from a point source? (2) What factors influence seed deposition at both the sub-reach (< 100 m) and reach (> 100 m) scales? (3) What is the loss rate of fluvially dispersed seed? (4) Is there a higher level of vegetation cover at places along the bank that have higher trapping efficiency?

5.3 Methods

5.3.1 Study site

Three study sites were selected in the Wingecarribee catchment of southeastern Australia (Figure 5.1) because of the greater rainfall and security of flows in this catchment. The Wingecarribee River site, the largest of the channels, had a mean channel width of 23 m over the 5 km experimental reach. The study site was located near the head of the river, stream order two (Strahler 1952), just outside the township of Bowral. The river is highly regulated, because it is used for interbasin transfers for urban consumption, resulting in most of the flow being derived from the headwater dam and ultimately the Shoalhaven River. The average discharge is 454 MLd^{-1}, fluctuating between 12 MLd^{-1} and 10 000 MLd^{-1}. The experimental zone passed though grazing land with recently planted riparian tree and shrub cover of *Eucalyptus* and *Leptospermum* species. The other two sites are both tributaries of the Wingecarribee River - Joadja Creek and Black Bobs Creek. These sites on the two tributaries were 0.5 km long, on free-flowing waterways. The channel widths varied from 1 to 15 m, with discharge fluctuating between 0.00001 MLd^{-1} and 1 200 MLd^{-1}. The Joadja Creek site was on a 4th order stream reach, with a continuous riparian zone dominated by tree species of *Eucalyptus*, *Casuarina* and *Acer* (an alien

species), and *Leptospermum* and *Acacia* shrubs as a midstorey. Black Bobs Creek was located on a 4th stream order reach, and passes mainly through agricultural land, but with fragmented riparian stands of *Eucalyptus* and *Casuarina* trees.

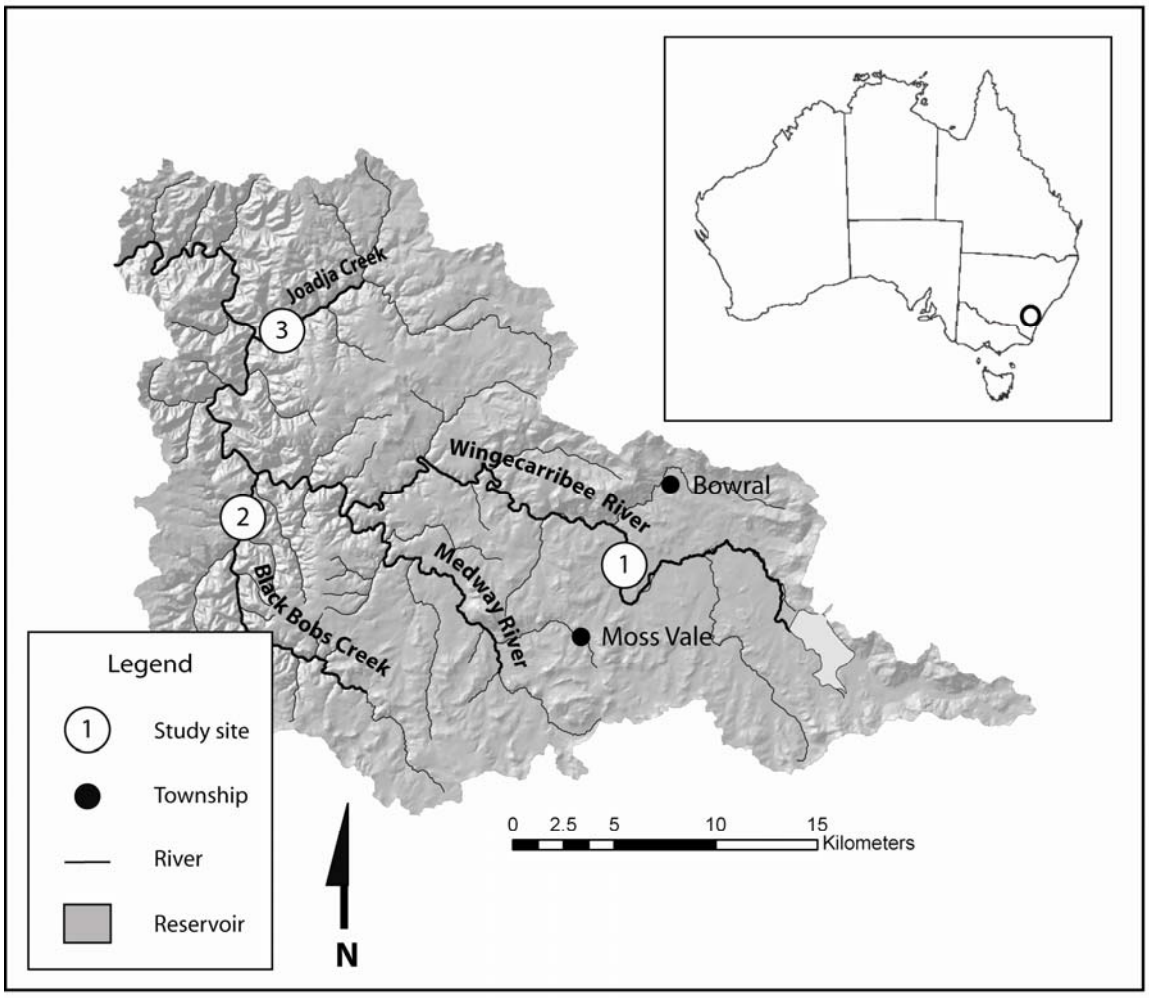

Figure 5.1 Location of study sites in the Wingecarribee catchment, New South Wales, Australia

5.3.2 Fluvial dispersal kernel of achenes

To determine the distance that fluvially dispersed buoyant seeds are transported, Helianthus annuus (sunflower) achenes were used (Andersson et al., 2000b; Merritt and Wohl, 2002). Although sunflower seed have different morphologies and buoyancies from many native Australian species the difference in dispersal kernel would probably be minimal; Anderson, Nilsson et al (2000) found little difference in dispersal between wooden cubes and Helianthus annuus seeds.The achenes were sterilised by heat and then colour coded to distinguish between replications. Multiple release points were used along the Wingecarribee River and the two tributaries to emphasize variations in the river bank factors that were determined to influence seed deposition and to reduce counting error.

Replicates were released at each release point (Table 5.1). The achenes were released in the centre of the stream, with a 15 minute gap between the replicate releases. The first series of releases was carried out in October 2007 (release 1) and replicated in the tributaries in November 2007 (release 2). The second release in the tributaries was done to determine the effect of flow on parameters of the dispersal kernel. Nets were positioned at the end of each study reach to catch seeds dispersing outside the survey area. Twenty-four hours after release the river banks were searched for deposited *H. annuus* achenes. Only those achenes that had deposited on the bank were counted, with the number within each sub-reach recorded as being deposited in a pool, riffle or backwater section. Survey stakes, previously placed, and global positioning receivers (Garmin GPSII) were used for reference to measure the river distance from the release point to the point of deposition. Discharge was measured at a gauging station on the Wingecarribee River and using a water velocity meter (FLO-MATE 2000) for the two tributaries.

Table 5.1 Design for the *Helianthus annuus* (sunflower seed) release experiment in the Wingecarribee River, Black Bobs and Joadja Creeks, southeastern Australia

Watercourse	Study reach length (m)	No. of releases	Release points (m)*	Replication per point	Seeds per replicate
Wingecarribee R.	5000	1	5 000	2	40 000
			4 000	2	40 000
			3 000	2	40 000
Joadja Ck.	500	2	500	2	10 000
			200	3	1 000
			100	3	1 000
			50	3	1 000
Black Bobs Ck.	500	2	500	2	10 000
			200	3	1 000
			100	3	1 000
			50	3	1 000

*Release point distance above the end of reach

5.3.3 Potential loss of achenes

A 24 hour float time test was used to determine the floating capacity of *H. annuus* achenes. Six replicates of twenty achenes were floated in plastic containers (15 x 10 x 5 cm). The number of achenes that were still floating was recorded every 2 hours for the first 8 hours, then 12 and 24 hours after the experiment commenced. The water in the trays was stirred vigorously and left for 10 minutes before each count.

Similarly painted *H. annuus* achenes were tested to determine if paint influenced their floating ability. The experiment corresponded in design to the floating ability of the unpainted *H. annuus* achene experiment, with six replicates of all 11 colours that were used in the achene release experiment.

To control for possible predation by birds, small mammals or insects over the 24 hours of the seed release experiments, *H. annuus* achenes were placed on the river bank at each release site. At the time of the achene release, three random sites within 20 m of the release site were used to determine if seed would be lost to predation. Ten achenes of random colour were placed on a disc at each site. Upon completion of the search for the released *H. annuus* achenes along the river banks, the number of achenes remaining at each control site was counted.

5.3.4 Hydrological and physical factors influencing seed aggregation

A survey of the river was carried out to quantify the factors that may influence seed deposition. The main factors assumed to influence deposition were macro factors water velocity, erosion, channel variability and sinuosity; and micro factors: large woody debris (LWD), and macrophyte cover (Johansson and Nilsson 1993; Andersson *et al.* 2000; Riis and Sand-Jensen 2006). Survey stakes were placed along the Wingecarribee River and its tributaries at 100 m and 20 m intervals respectively, using a differential global positioning system (Trimble L1 system) and total station (Leica TCR407), depending on the canopy cover and access. These sub-reaches (100 m and 20 m) were the same scale used to survey the biotic and abiotic factors that may influence seed deposition. Water velocity was calculated by measuring the cross-sections of channels between the survey stakes. At each cross-section, depth was measured at intervals of 1/5 of the river width. Discharge was measured at a gauging station on the Wingecarribee River and using a water velocity meter for the two tributaries. Erosion, LWD and aquatic vegetation were surveyed and classed from Manning's *n* tables (Cowan 1956; Gordon *et al.* 1999). Channel variability was calculated by measuring the wet perimeter at ¼ intervals of each sub-reach using a range finder (OPTi-LOGIC 600XL) or tape measure, depending on the channel size. Sinuosity was calculated by remote sensing via GIS (Arc 9.1) from aerial photos.

5.3.5 Riparian zone vegetation cover

Vegetation cover was recorded concurrently with the channel roughness survey. The survey was carried out at the same scales as previously described for channel roughness. Vegetation life form was classified using a Muir's table (Muir 1977). Plant cover of trees, shrubs and herbs was estimated using Braun-Blanquet classification (Braun-Blanquet 1932) and classed by the percentage cover of each sub-reach.

5.3.6 Data analysis

To analyse achene dispersal the 50^{th}, 90^{th} and 100^{th} percentiles were calculated to describe the dispersal distance. Manning's *n* was calculated for the length of each reach.

To assess the impact of water velocity, channel size and stream roughness (Manning's *n*) on the distance seed dispersed at the reach scale, model selection was used based on information theory and Akaike's Information Criterion (AIC) (Burnham and Anderson 2001) (R v2.5.0). Eight exponential models were tested on the 50, 90 and 100 percentile achene dispersion data (Table 5.3). All models were ranked according to the AICc value, with the best model having the lowest AICc.

Odds ratio was used to calculate the effect that environmental variables had in causing seed to aggregate at the sub-reach scale (SPSS v16). The Exp(β) parameter estimate shows for every unit increase in the odds ratio that there is an equal rise in the chance of seed deposition (versus non-deposition) within the sub-reach. An odds ratio of 1.0 indicates the environmental factor had no influence in causing seed deposition, while a variation absolutely larger than ±1 demonstrates a large effect. An odds ratio of >1.0 shows a positive effect and <1.0 a negative. To compare the significance that each environmental variable made in influencing seed deposition per study reach, the output from the logistic regression was converted to partially standardised coefficients (PSC)

$$PSC = e^{\beta.SD} \qquad (1)$$

where β is the raw coefficient and *SD* is the standard deviation of the environmental variable. For the statistical analysis all values were standardised. The data were weighted by the number of achenes that were deposited in each sub-reach. The covariates were

distance and the environmental variables derived from the river bank survey. Erosion was not included in the calculation for Joadja Creek as there was no variability between sub-reaches. Odds ratios were calculated for each release site along the Wingecarribee River. However, for the two tributaries all the release sites were grouped per release date to increase the power of the analysis. To determine the significance of pool, riffle and backwater on seed deposition a single factor ANOVA was used. If a significant result arose, a Tukey-Kramer multiple comparison test was carried out.

The influence of paint on the float time of *H. annuus* achenes was analysed using a single factor ANOVA, as previously described. The analysis included all eleven colours and the unpainted achenes. The analysis was carried out for all time periods that were recorded. For the predation data, logistic regression was used to analyse the data, since 100% loss rate occurred at all sites where achenes were taken.

5.4 Results

5.4.1 Survey reach variables

The Wingecarribee River study reach was >4x as wide and had up to several orders of magnitude higher water velocity than the tributaries (Table 5.2). The larger of the two tributaries, Joadja Creek, had three times more channel area than Black Bobs Creek. Water velocity at the time of achene release was higher on Joadja Creek than Black Bobs Creek, whereas the water velocity at the time of the second release on Black Bobs Creek was comparable to Joadja Creek's first release (Table 5.2).

5.4.2 Wingecarribee River dispersal kernel

Less than 10% of achenes released were retrieved along the Wingecarribee River and the dispersal distance ranged from 400 m to 600 m (Table 5.2). The deposition of the *H. annuus* achenes showed high aggregation near the release point with a long right-skewed tail (Figure 5.2). Over 90% of the achenes were deposited within 2000 m of the release site, with the furthest travelling 4500 m. The variability of the dispersal kernel in relation to the replicates was generally low (Table 5.3). However, variability was high between release sites, potentially showing the effect of sub-reach scale environmental factors such as LWD influencing the dispersal distance. Environmental factors such as

channel variability may also explain the shorter dispersal kernel for the 3000 m reach even though the sub-reach had the highest water velocity (Table 5.2).

5.4.3 Joadja Creek dispersal kernel

More than twice the proportion of *H. annuus* achenes were retrieved from Joadja Creek (>20%) compared with the Wingecarribee River, and over half of them were deposited within 80 m of the release point (Figure 5.2). Water velocity at the time of the second release was 0.22 ms^{-1} higher than the first, reflected by the longer dispersal kernel and more achenes depositing in the nets at the end of the reach (Table 5.2). The variability in the dispersal curve between the replicate releases was low, with the standard error in many cases zero. The main discrepancy was at the 200 m site, the dispersal kernel being up to 60% shorter than the other release sites, with the exception of the furthest dispersed achene. In this instance one achene dispersed 180 m, while the majority were deposited close to the point of release.

5.4.4 Black Bobs Creek dispersal kernel

Retrieval of achenes in Black Bobs Creek ranged from 10 - 60% (Table 5.2), with over 90% of those retrieved depositing within 100 m of the release point (Figure 5.3). Only the 500 m site (Release 2) categorically had achenes dispersing beyond this distance. However, achenes released in the 50 m reaches could have dispersed further, but the nets at the end of the reach impeded their movement. Overall fewer achenes were collected in the nets at the end of this reach than for Joadja Creek, indicating a shorter dispersal kernel (Table 5.2). Water velocity differed by 0.3 ms^{-1} between the two release dates, resulting in a 30 - 50% increase in dispersal distance. However, some of the dispersal curves were shorter despite higher water velocity; potentially caused by inundation of sub-reach scale geomorphological features and riparian areas that increased trap efficiency.

Table 5.2 Spatial averages for flow and channel dimensions along the Wingecarribee River, Joadja Creek and Black Bobs Creek; river variables: mean water velocity ($\overline{V}$), average width ($\overline{W}$), average depth ($\overline{D}$), and their respective standard deviation, which were calculated from cross-sections of the channels at 100 m (Wingecarribee R.) and 20 m (tributaries) intervals; also summarised are the results of the *Helianthus annuus* achenes release experiment: the percentage of seed recovered and caught in nets (at the end of the experimental reach), and the average distance that 50th, 90th and 100th percentile (D50, D90 and D100 respectively) of the *H. annuus* achenes were transported and their respective standard error (SE)

Water course	Release site (m)	$\overline{V}$	$\overline{W}$	$\overline{D}$	Seed found (%)	Seed caught in nets (%)	D50 distance	D90 distance	D100 distance
Wingecarribee River	Combined sites				8.1 ± 1.1	0.0	533 ± 95.5	1533 ± 164.7	3750 ± 284.9
	5000	0.94 (0.50)	23.1 (11.79)	1.30 (0.41)	10.2 ± 1.8	0.0	300 ± 100.0	1950 ± 150.0	4500 ± 100.0
	4000	0.95 (0.42)	24.7 (14.12)	1.20 (0.55)	8.7 ± 0.7	0.0	800 ± 0.0	1500 ± 0.0	3850 ± 50.0
	3000	0.98 (0.46)	24.0 (16.31)	1.20 (0.37)	5.3 ± 0.4	0.0	500 ± 0.0	1150 ± 250.0	2950 ± 50.0
Joadja Creek (Release 1)	Combined sites				23.4 ± 1.0	12.0			
	500	0.15 (0.13)	5.5 (3.07)	0.55 (0.77)	22.7 ± 0.1	0.0	60 ± 0.0	80 ± 0.0	100 ± 0.0
	200	0.20 (0.14)	5.4 (2.77)	0.31 (0.21)	24.7 ± 1.8	0.0	20 ± 0.0	40 ± 0.0	106 ± 46.7
	100	0.18 (0.11)	6.9 (3.10)	0.39 (0.27)	20.8 ± 1.7	1.3 ± 0.2	60 ± 0.0	73 ± 6.7	*>100 ± 0.0
	50	0.17 (0.11)	7.0 (4.31)	0.54 (0.26)	25.5 ± 0.5	32.4 ± 1.5	40 ± 0.0	*>50	*>50
Joadja Creek (Release 2)	Combined sites				22.8 ± 3.6	34.6			
	500	0.37 (0.15)	5.5 (3.07)	0.65 (0.91)	22.1 ± 2.3	0.0	60 ± 0.0	90 ± 8.2	360 ± 0.0
	200	0.39 (0.18)	5.4 (2.77)	0.37 (0.25)	6.1 ± 1.8	26.4 ± 0.0	40 ± 6.7	*>200	*>200
	100	0.38 (0.06)	6.9 (3.10)	0.46 (0.32)	29.0 ± 1.5	38.6 ± 0.2	80 ± 6.7	*>100	*>100
	50	0.36 (0.50)	7.0 (4.31)	0.64 (0.10)	34.0 ± 3.2	61.8 ± 2.2	*>50	*>50	*>50
Black Bobs Creek (Release 1)	Combined sites				44.7 ± 6.3	0.0			
	500	0.002 (0.002)	3.1 (1.56)	0.20 (0.14)	62.0 ± 1.4	0.0	40 ± 0.0	40 ± 0.0	60 ± 0.0
	200	0.003 (0.002)	3.6 (1.17)	0.24 (0.13)	44.6 ± 2.4	0.0	40 ± 0.0	80 ± 0.0	100 ± 0.0
	100	0.002 (0.001)	4.0 (0.72)	0.20 (0.17)	58.5 ± 6.3	0.0	33 ± 6.7	47 ± 6.7	67 ± 6.7
	50	0.003 (0.001)	4.0 (0.91)	0.18 (0.10)	13.5 ± 0.6	9.2 ± 1.9	40 ± 0.0	*>50	*>50
Black Bobs Creek (Release 2)	Combined sites				21.8 ± 3.9	13.8			
	500	0.31 (0.18)	3.5 (1.56)	0.26 (0.14)	43.9 ± 0.6	0.0	60 ± 0.0	80 ± 0.0	120 ± 0.0
	200	0.32 (0.16)	4.2 (1.17)	0.28 (0.13)	13.4 ± 2.1	0.0	60 ± 0.0	80 ± 0.0	93 ± 13.3
	100	0.31 (0.17)	4.4 (0.72)	0.27 (0.17)	20.4 ± 1.4	0.2 ± 0.2	20 ± 0.0	27 ± 6.7	40 ± 0.0
	50	0.34 (0.15)	4.4 (0.91)	0.24 (0.01)	9.6 ± 0.9	61.9 ± 1.0	*>50	*>50	*>50

*Distance greater than the survey reach

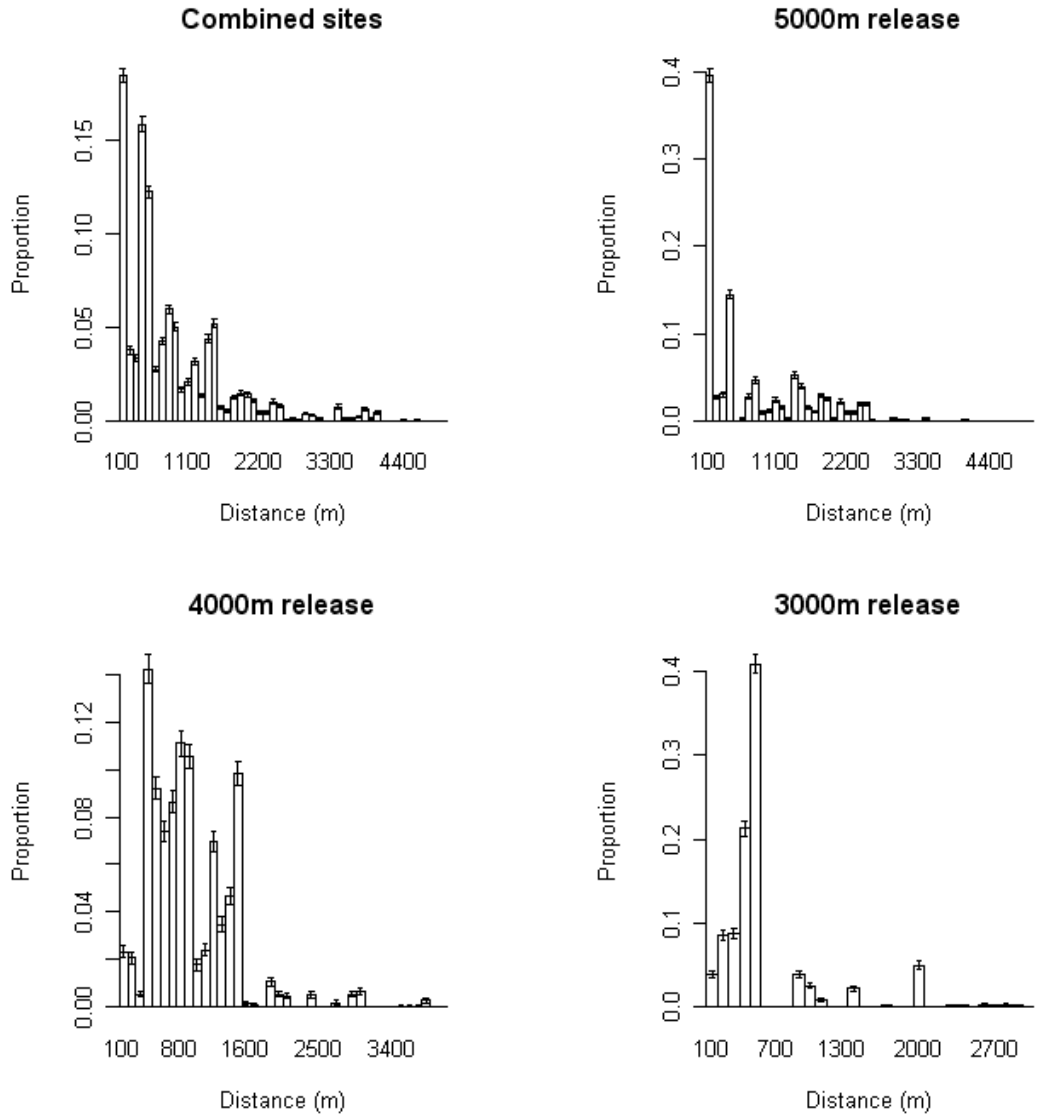

Figure 5.2 The distribution of *Helianthus annuus* achenes found over a 5000 m reach along the Wingecarribee River, southeastern Australia; combined site refers to the aggregation of all three release sites; 5000 m, 4000 m and 3000 m release refers to the release distance upstream from the end of the reach from which the achenes were released

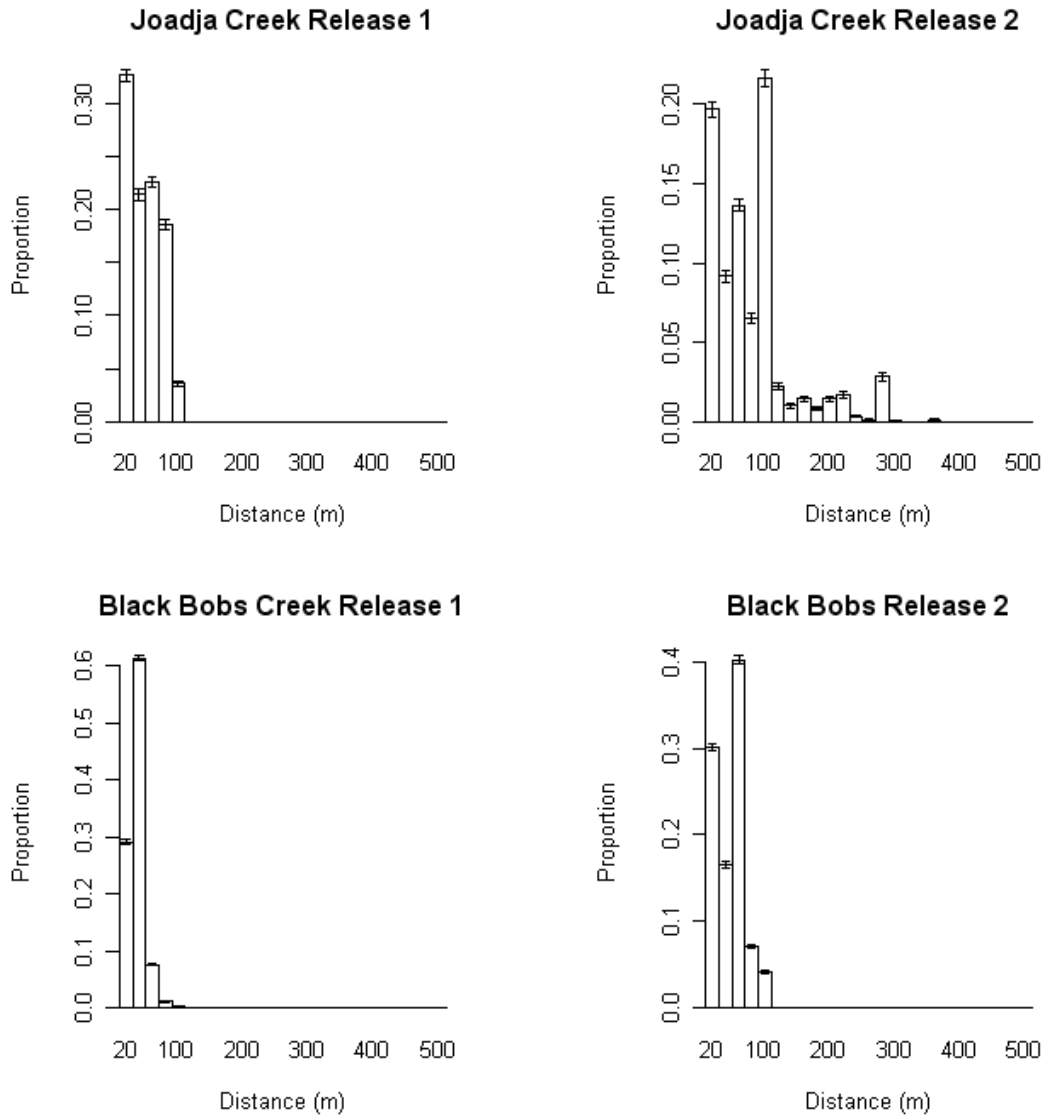

Figure 5.3 The distribution of *Helianthus annuus* achenes found over 500 m reaches along the Joadja Creek and Black Bobs Creek, southeastern Australia; the distribution is from combined data of all four release sites: 500 m, 200 m, 100 m and 50 m (which refers to the release distance upstream from the end of the reach); achenes that dispersed outside the survey reach are not included

5.4.5 Potential loss of seed

The average number of floating *H. annuus* achenes after 24 hours in the water was <60%, although after 8 hours it was >80%. The difference between the floating ability of painted (all eleven colours) and unpainted *H. annuus* achenes was not significant ($F = 1.8$; df = 11, 60; $P = 0.08$). Therefore there was no influence of paint or a particular colour on the ability of the achenes to float.

There was a 17.5% loss rate of *H. annuus* achenes over the 24 hour predation experiment. All sites that lost achenes had a 100% loss rate. However, the influence of predation was not significant ($n = 57$, $P = 0.7$) over all sites.

5.4.6 Hydrological and physical factors influencing seed aggregation

Water velocity, channel width and channel roughness (Manning's *n*) comprised the most supported model in describing seed dispersal distance at the reach scale (Table 5.3). At the sub-reach scale all biotic and abiotic factors that were surveyed for their influence on seed deposition were found to be significant ($P < 0.001$), except for channel variability and aquatic vegetation (Wingecarribee 4000 m release) (Table 5.4). However, there was variability in the influence each factor had on trapping achenes in comparison to the different release sites and flow levels. The odds ratio values varied by ±0.07 from one, meaning that there was only a small increment or decline in their influence to trap seed for every unit increase in the factor, with the exception of one or two outliers for each factor (Table 5.4). For instance, channel variability had an odds ratio of achene deposition (versus non-deposition) ranging from 0.99 - 1.06. The exception was along the Wingecarribee River (3000 m release), which had an odds ratio of 1.40 indicating for every one unit increase in channel variability the chance of deposition increases by 40%. Erosion and aquatic vegetation were the most variable factors with odds ratios ranging from 0.97 to 9.31, and 0.80 to 9.68 respectively.

The number of achenes deposited in a pool, riffle or back-water were found to be significantly different ($F = 28.5$; df = 2, 147; $P < 0.0001$). Pool and riffle sites were found to be significantly different (Tukey-Kramer; $P < 0.0001$). However, there was no significant difference between back-water and riffle sections in the retention of achenes (Tukey-Kramer; $P < 0.7$).

Table 5.3 The top four models predicting fluvial seed dispersal distance at the reach scale for the 50th, 90th and 100th percentiles, in the Wingecarribee River and two tributaries, southeastern Australia

Parameter	Rank	-2 log likelihood	[1]K	[2]AICc	[3]ΔAICc	[4]W*i*
50th percentile						
Exp(Velocity, Manning's *n*, Width)	1	36.288	6	78.702	0.000	1.000
Exp(Manning's *n*, Width)	2	36.287	5	80.574	17.998	0.000
Exp(Velocity, Manning's *n*)	3	36.288	5	80.576	18.000	0.000
Exp(Velocity)	4	36.351	4	82.576	32.125	0.000
90th percentile						
Exp(Velocity, Manning's *n*, Width)	1	20.603	6	50.954	0.000	1.000
Exp(Velocity, Manning's *n*)	2	21.477	5	51.206	2.161	0.339
Exp(Manning, Width)	3	30.525	5	58.339	20.256	0.000
Exp(Velocity)	4	26.170	4	69.049	25.546	0.000
100th percentile						
Exp(Velocity, Manning's *n*, Width)	1	27.076	6	60.152	0.000	1.000
Exp(Velocity, Manning's *n*)	2	28.563	5	63.125	20.973	0.000
Exp(Manning's *n*, Width)	3	30.960	5	63.126	25.768	0.000
Exp(Velocity)	4	28.563	4	69.920	34.974	0.000

[1]Number of parameters estimated in each model
[2]Akaike's Information criterion adjusted for small sample size
[3]The difference between the AIC value for a particular model and the AIC value for the best model calculated
[4]Akaike weight, probability that the model is the best between considered models

Table 5.4 The influence of abiotic and biotic environmental factors that may cause seed aggregation along the Wingecarribee River, Joadja Creek and Black Bobs Creek; summarised are the results from logistic regression model: model constants, and Partially Standardised Coefficients (PSC), significance level (*P*) and the odds ratio (Exp(β)) of six variables

Water course	Const.	Velocity			Erosion			Channel Variability			LWD			Aquatic Vegetation			Sinuosity		
		PSC	P-value	Exp (B)	PSC	P-value	Exp (B)	PSC	P-value	Exp (B)	PSC	P-value	Exp (B)	PSC	P-value	Exp (B)	PSC	P-value	Exp (B)
Wingecarribee R. (5000 m)	-2.095	1.001	<0.001	1.00	0.424	<0.001	9.31	1.346	<0.001	1.06	0.615	<0.001	0.98	1.479	<0.001	1.02	1.216	<0.001	1.01
Wingecarribee R. (4000 m)	-0.387	0.639	<0.001	0.99	7.312	<0.001	0.97	1.029	0.170	1.01	0.029	<0.001	0.98	1.042	0.051	1.00	0.907	<0.001	0.97
Wingecarribee R. (3000 m)	0.314	0.000	<0.001	0.98	1.317	<0.001	1.03	1.079	<0.001	1.40	0.003	<0.001	0.93	0.439	<0.001	0.97	1.805	<0.001	1.04
Joadja Ck. (1)	-3.393	0.995	<0.001	0.98	N/A	N/A	N/A	0.912	0.040	0.99	1.682	<0.001	1.02	1.228	<0.001	1.01	1.052	<0.001	1.01
Joadja Ck. (2)	-0.871	1.000	0.011	1.00	N/A	N/A	N/A	0.806	<0.001	0.99	1.275	<0.001	1.01	0.540	<0.001	9.68	0.942	<0.001	0.99
Black Bobs Ck. (1)	-4.372	1.001	<0.001	1.50	1.317	<0.001	1.34	1.140	<0.001	1.01	0.343	<0.001	0.96	3.377	<0.001	1.06	1.074	<0.001	1.02
Black Bobs Ck. (2)	-8.193	1.019	<0.001	1.03	1.178	<0.001	5.64	0.770	<0.001	0.99	2.086	<0.001	1.02	0.006	<0.001	0.80	1.063	<0.001	1.02

*Release 1 (October 2007) and 2 (November 2007)

Table 5.5 The relationship between vegetation classes being present at places of seed aggregation along the Wingecarribee River, Joadja Creek and Black Bobs Creek; summarised are the results from a logistic regression model: the model constants (*C*), logistic regression coefficient (β), significance levels (*P*) and odds ratio (Exp(β))

		Native vegetation			Tree			Shrub			Herb		
Water course	*C*.	β	P-value	Exp (β)	β	P-value	Exp (β)	β	P-value	Exp (β)	β	P-value	Exp (β)
Wingecarribee R.	-1.893	0.01	<0.001	1.011	0.06	<0.001	1.059	-0.05	<0.001	0.995	-0.01	<0.001	0.993
Joadja Ck. (*1)	2.439	-0.06	<0.001	0.943	-0.19	<0.001	0.830	0.15	<0.001	1.163	0.07	<0.001	1.067
Joadja Ck. (*2)	-0.368	-0.04	<0.001	0.964	-0.05	<0.001	0.953	0.01	<0.001	1.013	0.12	<0.001	1.127
Black Bobs Ck. (*1)	-6.014	0.20	<0.001	1.221	0.06	<0.001	1.062	0.03	<0.001	1.026	-0.36	<0.001	0.697
Black Bobs Ck. (*2)	-0.262	0.18	<0.001	1.191	0.14	<0.001	1.148	-0.06	<0.001	0.945	0.31	<0.001	1.361

5.4.7 Relationship between achene deposition and riparian zone vegetative cover

The deposition of achenes was a significant predictor of vegetative cover (Table 5.5). Seed deposition increased in areas of more native vegetation and tree cover along Wingecarribee. However, Joadja Creek had more achene deposition in areas of greater shrub and herb cover. The higher trapping ability along Joadja Creek compared to the other two channels may be because of the greater amounts of intact native foliage along the channel banks of the river.

5.5 Discussion

5.5.1 Fluvial dispersal kernel of achenes

Fluvial seed dispersal kernels have a similar distribution to many other plant dispersal methods (Clark *et al.* 1998; Abe *et al.* 2006). *H. annuus* achenes were highly aggregated close to the release point with a long right-skewed tail (Figure 5.2; Figure 5.3). With increased water velocity the mean deposition distance is moved further down the river channel, thereby flattening the distribution curve. This dispersal kernel is similar to that found previously (Johansson and Nilsson 1993; Andersson *et al.* 2000; Vogt *et al.* 2004; Riis and Sand-Jensen 2006). Rhizomes released in the Saver River showed a leptokurtic dispersal, with most found within 1.5 km of the release point, and the furthest dispersing 3 km (Johansson and Nilsson 1993). The dispersal kernel was also similar to that found in studies of anemochory (wind dispersal) (Clark *et al.* 1998) and zoochory (dispersal by animals) (Abe *et al.* 2006), and with the movement of fluvially dispersed point source pollution (Fischer *et al.* 1979). The main portion of the seed dispersal curve can be well defined, but quantifying the dispersal distance of the outliers has been more challenging to resolve.

A few outliers are capable of dispersing long distances, increasing the extent of a species. However, it has been challenging to track outliers that may move 100s of kilometres from their source (Greene and Johnson 1995; Bullock and Clark 2000). Over a short period (24 hrs) the distance that the outliers were transported could be more accurately quantified than over longer release periods. The furthest achenes were transported 15x the average dispersal distance, showing the potential capacity for long distance dispersal of a few outliers even at low flows (Table 5.2). Whereas, over a two week release period some seed

mimics were found up to 150 km from their release point, but it was not known how far the furthest dispersed (Andersson *et al.* 2000). The implications of plants being able to disperse so far are shown by species such as the introduced species *Alternanthera philoxeroides* (alligator weed), which can quickly invade a whole river system (Burgin and Norris 2008). To mitigate the impact of such species there is a need to understand the main factors that cause their rapid spread.

Water velocity, channel width and roughness (Manning's n) were all important factors in controlling the seed dispersal curve at the reach scale (Table 5.4). Linear increases in these factors caused exponential changes in the dispersal curve as defined by the best fitting model. Augmentation of shear stress and fewer dead zones result in longer dispersal in relation to water velocity and bank roughness, whereas larger rivers have less contact with the river bank (Riis and Sand-Jensen 2006). Other studies have shown similar relationships; an exponential increase in the dispersal distance in relation to water velocity was found along the Vindel River, Sweden (Andersson *et al.* 2000). Likewise, released plant fragments dispersed 2.5 times as far with a 100% increase in water velocity, and orders of magnitude with a doubling of channel width, Denmark (Riis and Sand-Jensen 2006). However, at a finer scale the influence of all these factors was more ambiguous.

At the sub-reach scale there was no clear relationship between water velocity and achene aggregation. Generally a neutral relationship was found, with the exception of Black Bobs Creek (Table 5.4). This result differs from what was expected, our results from the reach scale analysis and what has previously been reported (Schneider and Sharitz 1988; Danvind and Nilsson 1997; Merritt and Wohl 2002). However, there was a significant difference in achene deposition between pool and riffle sections, which is analogous to water velocity. This finding is comparable to the significant difference in seed deposition found between low-flow areas (e.g. pools and slack waters) and high water velocity areas (e.g. straight reaches and cut banks) (Merritt and Wohl 2002). The difference in the results between water velocity and pool-riffle sequences may be to do with the scale at which they were recorded where the pool-riffle data were recorded at a finer resolution.

The variability in the trapping ability of environmental factors at the sub-reach scale may be caused by changes in other factors such as water level. Sinuosity and LWD did not markedly change between rivers and release times (Table 5.4), because these variables would not be affected by an increase in water level. Alternatively, the trapping capacity of

aquatic vegetation may vary with greater water depth and/or slower plant growth rates at the time of seed release, resulting in the high variability observed (Table 5.4). Submerged vegetation cover was shown to have influenced the retention of non-floating propagules, but had minimal effect on floating propagules, along four lowland streams in Denmark (Riis and Sand-Jensen 2006), thereby showing the influence channel depth and seasonality can have on seed retention.

5.5.2 Potential loss of seed

Predation and sinking, of short floating seed (<1 day), could potentially be the major sources of seed loss during dispersal. Post-dispersal predation by insects (Pettit and Froend 2001), rodents (Schreiner *et al.* 2000) or birds (Holmes and Froud-Williams 2005) can influence regional vegetation structure because certain areas may be highly grazed or particular seeds may be preferentially consumed (Janzen 1971; Cavers 1983; Hulme 1998). The occurrence of total loss or no loss of *H. annuus* achenes observed at our control sites illustrate how this may occur. If seeds are deposited within the home range of a small rodent they may become highly preyed on, whereas other deposits of seeds in an adjacent sub-reach, 20 m away, maybe left untouched, such as between the control sites. This high level of predation could mean that, even if a position along the channel was advantageous for germination, because of granivores, a plant species may not be able to establish (Hulme 1998). Predation did not significantly reduce the number of *H. annuus* achenes across the study reaches. However, at the local scale it showed how the fecundity of highly preyed on species may be affected and the importance of long-distance seed dispersal so that diaspores may move away from the highest predated areas (Janzen 1971).

The number of *H. annuus* achenes that sunk after 24 hours shows the potential loss of hydrochorous seeds during fluvial transport (Jansson *et al.* 2000; Andersson and Nilsson 2002), which relates to the many fluvially dispersed species that have seeds that have a short floating times (Andersson *et al.* 2000). The float time of *H. annuus* achenes after 8 hours was >80%, although after 24 hours it was <60%. However, taking into account water velocity along the research reaches most achenes would traverse the river sections in <8 hours, resulting in the lower loss rate. Even so, for naturally dispersing seed it has been found that their floating ability does not necessarily influence their abundance and dispersal range (Jansson *et al.* 2000; Nilsson and Svedmark 2002; Gurnell 2007).

Transportation periods can often be short, and seeds may go in and out of temporary storage during dispersal (Gurnell *et al.* 2007).

The two main potential sources of loss were from predation (17.5%) and sinking (58.5% after 24 hours); these two factors could account for most of the observed loss. However, the recovery rate is similar to that found by Andersson *et al*. (2000) who used wooden cubes that were more buoyant and were not edible. Even with this level of recovery the dispersal kernels were comparable between all releases, and results reflect what has been previously reported (Johansson and Nilsson 1993; Andersson *et al.* 2000; Vogt *et al.* 2004; Riis and Sand-Jensen 2006). Seed survival and thus the inputs into a reach are important in shaping riparian vegetation structure, but other environmental variables such as aspect, soil type and competition also influence species recruitment (van der Valk 1981).

5.5.3 Relationship between achene deposition and riparian zone vegetative cover

The relationship between achene deposition and vegetative cover changed both between river reach and releases. The variability may be because of external influences, such as lateral connectivity from upland plants. Such a strong correlation between upland and riparian vegetation communities was found along the Vindel River, Sweden (Renofalt *et al.* 2005). This correlation may occur because of other dispersal means, such as zoochory or anemochory, as well as hydrochory from overland flow, which can transport diaspores into a riparian zone (Garcia-Fayos *et al.* 1995; Pettit and Froend 2001; Renofalt *et al.* 2005). Overland movement of seeds have been shown with the use of turf seed traps, where the floodplains were the source of diaspores during the summer months along the Cole River, UK, transported either by wind, surface runoff or soil movement (Gurnell *et al.* 2006). Alternatively, the experiment and results from the Wingecarribee catchment illustrate one stage of dispersal at low flow, which does not take into account multi-phase transport. However, it does reflect rivers affected by regulation and lower flows (resulting from climate change), which will potentially decrease multiphase fluvial dispersal (Chambert and James 2009). This potential reduction in hydrochorous seed rain is one aspect that needs to be considered in rehabilitation and river management plans.

5.5.4 Management implications

River rehabilitation is driven in a large part by the need for re-establishment of riparian vegetation. Understanding the magnitude and composition of the seed rain entering a reach

may help determine the level of management that is required regionally. The prescribed method for revegetating a river is to start at the headwaters and work down. This is not always possible because of factors such as land access, jurisdiction and cost. Therefore, understanding the potential seed rain that might enter a downstream reach, the available amount of seed, its dispersal distance and its deposition probability, is important for estimating the susceptibility of an area to alien species infestation. Alternatively, if there are regionally significant stands of native species upstream from a rehabilitation site the possible influence of such stands on the downstream riparian vegetation structure through seed input may potentially be significant (Dalling *et al.* 1998).

Human induced changes are significantly altering the historical flow regime of rivers, potentially resulting in lower capacity to disperse seed. Many rivers are regulated, water is stored, releases are unseasonal and flows are reduced. These conditions are not amenable to seed transport, thus breaking the connectivity along rivers. Similarly, the predicted decline in flows in many rivers resulting from climate change, such as in southeastern Australia, may cause reductions in seed dispersal. Understanding the main drivers of fluvial seed dispersal and aggregation can help in planning mitigation strategies such as timed environmental flows and reducing barriers to aid connectivity between otherwise isolated patches of riparian vegetation.

The present results suggest that fluvially dispersed seed even at low flow can be transported several kilometres from their parent source in short periods, therefore aiding their recruitment by reducing intra-species competition from their cohort. However during this dispersal phase large quantities of seed may be lost through predation or sinking. Water velocity, channel dimensions and roughness influenced seed aggregation at the reach scale. However, the trapping ability of the stream at the sub-reach scale (<100 m) was variable between channels and water discharge. This may be because increased water level reduces the trapping ability of certain biotic and abiotic variables because they have less contact with the water surface, such as for macrophytes. Hydrochory is one method of dispersal that may influences riparian vegetation structure through inputs of both native and alien species

Chapter 6: Modelling of floating seed dispersal in a fluvial environment

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Chapter 6

Groves, J. H., Williams, D., Caley, P., Norris, R. H. & Caitcheon, G. (2009) Modelling of floating seed dispersal in a fluvial environment, *River Research and Applications*, 25: 582-592.

Chapter 7: Synopsis

7.1 Introduction

The aim of the study reported in this thesis was to *measure the spatio-temporal patterns of hydrochorous seed movement.* This aim was achieved. Clear spatio-temporal variation of the instream species pool was found to correlate between the sites, within the catchment, with seasonality being the main factor controlling instream seed abundance and species richness (Chapter 3). Variation was further reflected in the analysis of the hydrochorous seed sources (Chapter 4). The two main factors determining the dispersal kernel of hydrochorous seed were found to be water velocity and stream dimensions (Chapter 5), and deduced from results presented in Chapters 3 and 4. From understanding the main drivers that control fluvial dispersal and using the data presented in Chapter 5, a semi-empirical model of fluvial seed dispersal was developed (Chapter 6).

The spatio-temporal variability of the instream species composition, their potential sources and fluvial dispersal distance has been discussed in each chapter. This final chapter draws together all the previous findings and presents the major conclusions of the thesis.

7.2 Species occurrence in the water column

The study highlights the large number of species that use hydrochory to disperse. A total of 79 species and 11 577 viable seed were trapped at the six instream sampling sites over 17 months in the Wingecarribee catchment (Table 3.2); of these, >60% of the fluvially dispersing species were non-native to Australia (Chapter 3). A similarly high proportion of non-native species was also found from survey/sampling of the standing riparian vegetation, the soil seed banks and of aerially dispersed seed (Figure 4.4), indicating that non-native species have become established extensively throughout the riparian zone and that there is longitudinal connectivity of the river through the catchment potentially related to hydrochory.

7.3 Spatial variability

The results from instream sampling, vegetation surveys, soil seed bank estimates and aerial seed sampling at six sites throughout the Wingecarribee catchment fulfilled the objective of understanding the variability in hydrochorous seed rain and its sources through space.

7.3.1 Sources of propagules

Most seed were locally transported, depositing close to the parent source, during periods of low flow. A similar conclusion was reached for the importance of local dispersal from the results of several previous studies that investigated either hydrochory (Johansson and Nilsson 1993; Andersson *et al.* 2000; Vogt *et al.* 2004; Riis and Sand-Jensen 2006), anemochory (Clark *et al.* 1998) or zoochory (Abe *et al.* 2006). Floristic composition of the local riparian vegetation accounted for 75% of the variability of the instream species pool, with 90% of it taken into account from all local sources of seed that were surveyed (Table 4.3). The dispersal kernel derived from the release of seed mimics (Chapter 5) supported the findings that most seed only move short distances from their parent source (Table 5.2). The released sunflower achenes aggregated near the release point and their distribution had a long right-skewed tail that represented a few outliers. Diaspores from the local riparian vegetation were therefore proportionally more represented in the instream species pool (Table 4.3).

Species presence in the riparian zone was the main indicator that a species would be dispersed fluvially. The majority of the instream seed pool consisted of only a few species, namely *Casuarina cunninghamiana, Conyza bonariensis* and *Rumex crispus*, which together made up over half the total number of seeds collected from all sites. The 10 most abundant species made up three quarters of the instream species pool within the catchment (Table 3.2), and were the most abundant species in the riparian zone. If the quantity of seed a species fluvially disperses results in increased recruitment in the riparian zone, a positive feedback may be occurring for those riparian species that successfully use hydrochory. This was evident in the Wingecarribee catchment from the high representation of non-native species present that were hydrochorous and also found both in the riparian vegetation and in the seed banks (Table 4.3).

Capacity to fluvially disperse was not shown to be particular to the studied life-history traits. This result signifies that these plant life-history traits (Chapter 4) are not necessarily

an indication of hydrochory. Primary dispersal may occur through aerial or gravitational vectors acting directly into the channel or into the riparian zone seed bank where they may be better mobilised by over bank flows. Once in the water column, buoyant seed may be transported in the upper section of the column, but less buoyant species may adhere to other floating organic matter (Jansson *et al.* 2005) or else saltate along the bottom or even be held in a temporary store in the substrate and remobilised during periods of high flow (Gurnell *et al.* 2007). Many obligate and other riparian species may therefore prefer riparian zones for other environmental reasons such as close proximity of the water table and/or fertile soils, rather than the requirement for fluvial dispersal. However, hydrochory is a major benefit of growing in riparian habitats, which is another vector a species can use for dispersal and one that can facilitate long distance dispersal.

7.3.2 Influence of water flow rate

Water velocity was the main factor controlling the instream seed dispersal kernel (Chapters 3, 4 and 5). There was a positive correlation between water velocity and both species richness and instream seed density, with flooding in 2007 increasing the model fit (Table 3.5). Similarly, a positive correlation was found between water velocity and the number of non-local species (Table 4.5), thereby indicating that as velocity increases more diaspores were transported further. The dispersal kernels derived from the sunflower achene release experiment were significantly different in relation to water velocity when measured for three channels and at two flow levels (Table 5.2). The model of seed dispersal by water quantified the relationship between flow and dispersal kernel, using a power relationship (Equation 6.1) between seed transport distance and water velocity (Chapter 6). The dispersal experiment and predictions from the model showed that most seed were deposited close to the parent source although a few outliers may disperse longer distances.

There was limited fluvial connectivity of the Wingecarribee River at periods of low flow as shown by the experimental results presented in Chapters 3 and 4. At the catchment scale, the main groups that were identified from the cluster analysis of the instream species pool (Figure 3.4; Table 3.3) were divided spatially between the upper and lower catchments, reflecting different land use divisions within the catchment. This spatial division was further demonstrated by the sample results for standing riparian vegetation and for soil seed banks (Figure 4.3; Table 4.4). The secondary cluster analysis groupings (Figure 3.4;

Table 3.3) differentiated the instream species composition of the tributaries from those of the main channel, indicating local transport and deposition and that the seed derived from the tributaries did not contribute significantly to the species composition of the Wingecarribee River. There was no significant difference in species richness between the three tributaries, or between sites lower down the Wingecarribee River, although they differed in sub-catchment size, stream dimensions and land use (Table 3.1). If high connectivity was occurring throughout the catchment, species accumulation (Vannote *et al.* 1980) would be expected to be found, but most diaspores were evidently dispersing only locally.

Even at times of low flow outliers were fluvially dispersed long distances and this was evident from the proportion of the instream species pool that was not accounted for by local seed sources (Table 4.3). Similarly, the dispersal kernel of the released seed mimics was positively skewed with a few outliers in the Wingecarribee River travelling up to 4 km in 24 hours, and potentially further given more time (Table 5.2). However, most long distance dispersal was potentially occurring during periods of high flow.

At times of high flow, seed could be transported long distances (>80 km), potentially increasing connectivity between all the sampling sites (Chapters 3 and 4). More than twice as many species, as derived from the whole sampling season, were found in the lower catchment instream species pool compared with the number in the upper catchment or its tributaries, indicating that species were potentially dispersing down the catchment, but there was limited connectivity up the catchment (Chapter 3). During a flood peak (June 2007), 30% more species were caught in the lower catchment than in the upper catchment (Chapter 3). The significance of increased flow was shown by the results of the seed dispersal experiment which compared the seed dispersal kernel between the Wingecarribee River and its tributaries (Chapter 5). The quantification of the dispersal kernel was applied to the development of the semi-empirical model (Chapter 6). Thus it can be concluded that during floods are the times when most material is transported over the greatest distances.

Flood pulses are the main controlling factor for long distance transport of large quantities of propagules, as predicted by the flood pulse theory (Junk *et al.* 1989). This flood pulse theory originally described the lateral movement of biota onto a floodplain, but may also be significant to our understanding of the movement of material through a catchment (Boedeltje *et al.* 2004). Over periods of low flow most diaspores were dispersed less than

1 km from their point of release (Chapter 5) and were accounted for by local seed sources (<5 km) (Chapters 3 and 4), but the dispersal kernel increased in length by the power factor of water velocity (Chapter 5, and modelled in Chapter 6). Species richness, seed density and diaspore dispersal kernel all increased with water flow rate.

7.3.3 What influences seed deposition?

The biotic and abiotic factors that influence diaspores to be deposited were scale-dependent. At the sub-reach scale (<100 m) no clear relationship was found between the number of species that were deposited and the factors measured, although there was a significant difference between pool and riffle sections, thereby indicating that water velocity influenced deposition (Chapter 5). However, at the reach scale, water velocity, Manning's *n*, and stream dimensions all influenced seed aggregation (Table 5.3). Predicting the probability of fluvial seed depositing at a point can be done at the reach scale, but at a finer resolution such as at the sub-reach scale, each river needs to be quantified individually.

7.4 Temporal variability

The sampling of hydrochory and anemochory seed rain over 17 months fulfilled the objective of understanding the changes in species richness and seed density through time. The experimental results showed that the Wingecarribee River and its tributaries were seed limited. The main factor that influenced seed dispersal distance was water velocity, but seed availability from direct dispersal from vegetation or re-suspension of seed from temporary storage limited seed abundance in the instream species pool. Previously, temporal sampling of hydrochorous seed has been done only in the Northern Hemisphere. The northern winter and subsequent snow melt resulted in restricted winter sampling and different fluvial seed dispersal cycles (Andersson and Nilsson 2002; Vogt *et al.* 2004) than found in Southern Hemisphere evergreen habitats. Winter flooding in the Wingecarribee catchment was an important dispersal period for many species because it was the only time when there was flooding and thus greater connectedness. Temporal sampling of the instream species pool also showed changes in its composition and the shifts in the dominant source of seed through time.

7.4.1 Sources

Seasonality was the main limiting factor of seed availability for hydrochory. Significant increases in the instream species composition were measured in relation to the seed release timing of the riparian species (Figure 3.3); also as depicted in the updated concept model (Figure 7.1a) based on the original understanding of the sources of diaspores into the river system (Figure 1.1). During high seed release periods (autumn), there was only a weak relationship between the instream seed density and water velocity (Table 3.5); a stronger relationship was found during low seed release periods (winter, spring and summer). During periods of high seed availability large quantities of seed were deposited in the river channel and dispersed, whereas, when these seed were not available greater stream velocity resulted in more seed potentially being remobilised from temporary storage, such as in the river substrate or the banks.

The soil seed bank is a temporary seed store and a source that can be accessed during periods of higher flows, as shown by the difference between the concept models (Figure 7.1). During periods of low seed production (winter, spring and summer) the seed from the soil seed bank was the more dominant source of seed (Figure 4.2b). This was best illustrated by the cluster analysis results (Table 4.4) which showed that some of the soil seed bank samples were most similar to the instream species pool during the winter.

7.4.2 Seed depletion

Depletion of seed available for hydrochory may have occurred within the Wingecarribee catchment during the high flow (flood) event (Chapter 3), such as found with suspended sediment depletion within a fluvial environment (Walling and Webb 1982). Seed density and species richness decreased substantially in the month after the flood. Similarly, comparing results of seed germination between consecutive August months in 2007 and 2008, the instream seed density of the latter was generally considerably higher. Also, serotinous seed bank depletion may be the main reason why the soil seed bank became a more prominent seed source during seasons of low seed release (Chapter 4).

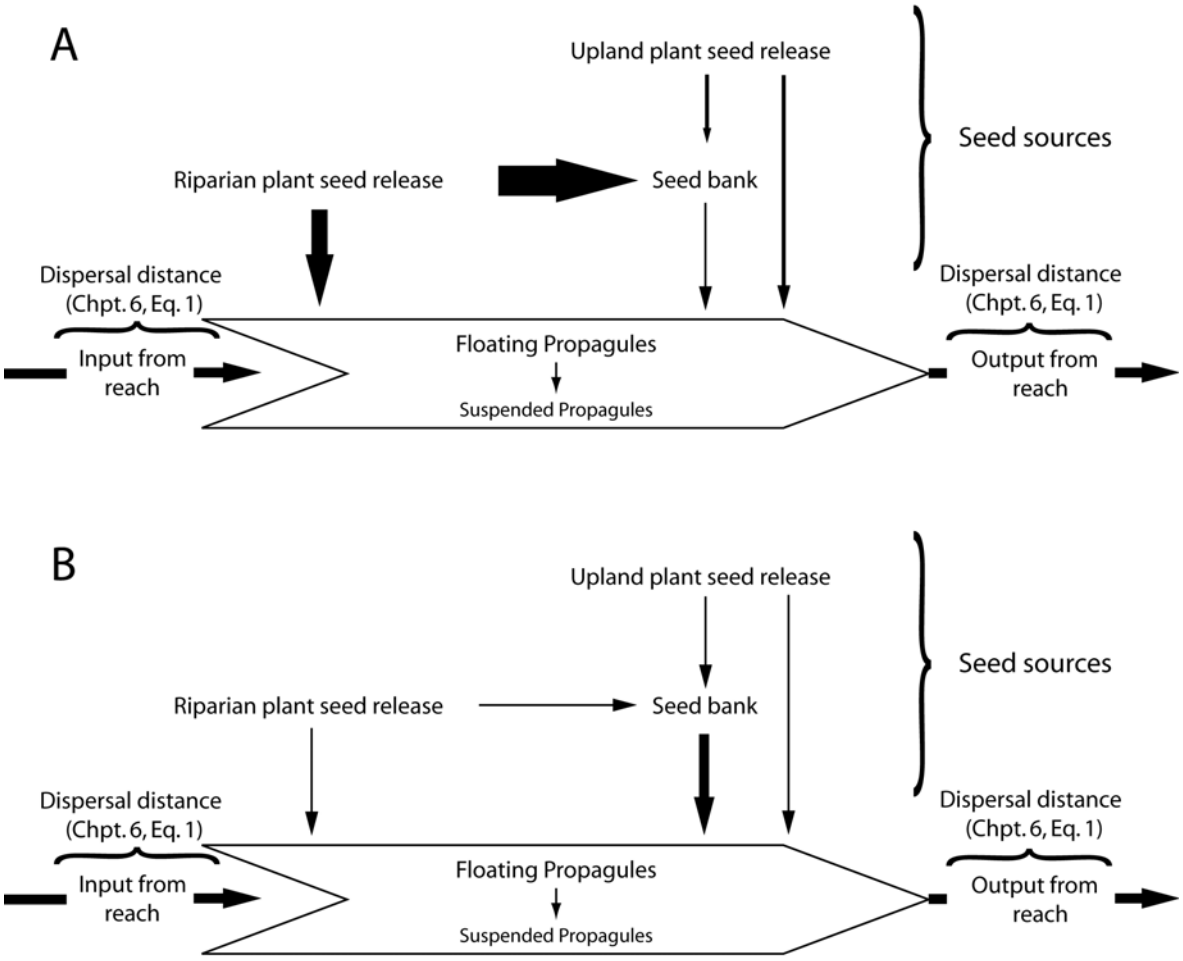

Figure 7.1 Conceptual model incorporating the changes in contribution of seed source between A) periods of high seed release in Autumn; B) low seed release periods in Winter, Spring and Summer; adjusted from the original conceptual model (Figure 1.1).

Depletion of the seed banks in an area may result in some species having less influence on new season recruitment locally. Therefore, early seeders, plants dispersing from upland or taller serotinous species may have an advantage over those species whose seed pool has been depleted during periods of high flow. Reduced competition for space, renewal of nutrients and replenishment of the water table all increase the fecundity of those species that enter the seed depleted area, thereby increasing their relative local abundance and forming a positive feed-back loop, which would change the structure and composition of the riparian vegetation.

7.4.3 Implications of the flood pulse concept

The limitation of the flood pulse concept in describing hydrochory through the catchment is that many rivers may be seed limited and seed source depletion may occur through a flood cycle. Therefore, there may be low seed density in the declining stage of a flood. Similarly, if multiple floods occur over a season there may not be sufficient numbers of propagules, especially at the head of the catchment, to mobilise and transport. This may apply similarly to the original flood pulse concept for lateral movement of propagules.

7.5 Predicting fluvial seed dispersal

The semi-empirical model presented in Chapter 6 fulfils the final aim of this thesis, namely to predict the dispersal curve of fluvially dispersed seed. It fits into the conceptual model (Figure 7.1) by predicting the proportion of seed rain that may enter a reach from any point upstream and the distance diaspores fluvially disperse downstream. Hydrological and aerial dispersal considerations were incorporated into the model, using stream velocity as the main driver for seed distribution, as described in Chapters 4, 5 and 6. The model used only core factors to predict the dispersal kernel, because over-parameterisation can increase the error margin and make model use difficult. The model predicted the dispersal kernel accurately over three river reaches of varying stream dimensions and velocities. This model is a key step in developing a catchment scale model of hydrochory because previous models used a negative exponential equation to describe seed movement through the catchment, which does not account for stream velocity, a key driver of hydrochory (Campbell *et al.* 2002; Levine and Murrell 2003).

7.6 Management implications

River restoration is driven in large part by the need to re-establish riparian vegetation for habitat conservation, bank stabilisation, and pollutant filtering. The optimal method for revegetating a catchment is to move from the headwaters down the catchment. This is not always possible because of land ownership or cost, as found in the Wingecarribee catchment. Therefore understanding the spatio-temporal patterns and sources of fluvially dispersed seed will help catchment managers and riparian restoration groups to better manage restored sites and areas of structurally intact native vegetation. This improved

management may arise because of increased understanding of the probability of non-native species dispersing into a reach. If there is a high chance of non-native species entering a restored reach, higher levels or active management might be applied over the first few years to increase the success rate of the restoration efforts. Alternatively, if there are high levels of native vegetation upstream that disperse fluvially, such as a stand of *Casuarina cunninghamiana*, passive management might be used to aid restoration by preparing the riparian zone to augment seed recruitment. Passive restoration such as this would reduce the cost of purchasing seedling stock, labour to plant, and guarantee a regional source of native plants. Understanding the composition and abundance of hydrochorous seed rain helps apply the appropriate level of management to riparian restoration projects.

Many non-native species have become integrated into the riverine environment (Chapter 4). Therefore for a comprehensive eradication program the target species needs to be removed not only from the target riparian zone, but also upstream, upland and from the soil seed bank (depending on species).

Most hydrochorous seed are locally dispersed, therefore comprehensive catchment management plans should include containment policies and procedures for 'Weeds of National Significance' (such as willows) and other non-native species to prevent them from becoming prolific throughout the environment at an early stage. The plan should include stakeholder education, professional support and early intervention. Working with the community and using early intervention will help to build community support and potentially save CMAs and governments millions of dollars in large-scale programs for weed control.

The effect of climate change is predicted to reduce average annual river flows in southeastern Australia, but the likelihood of more extreme storm events will cause larger irregular flood pulses. The research results in this thesis have shown the importance of high water velocity for long distance transport (Table 3.5). Therefore, many species in such plant families as Asteraceae and Poaceae that are able to store their diaspores in the soil seed bank will be able to take advantage of these irregular flood pulses, whereas other species which disperse their seed during a particular period, such as *C. cunninghamiana,* may be disadvantaged. The use of appropriately timed environmental flows is thus increasingly important for connectivity between otherwise isolated patches of native riparian vegetation.

7.7 Future research directions

Many new questions have arisen through the course of this study. The most striking research area that has been touched on but not developed is the linkage between fluvial seed dispersal to that of suspended sediment dynamics (Nilsson *et al.* 1993; Groves *et al.* 2007; Gurnell 2007; Gurnell *et al.* 2008). Such a linkage could potentially be achieved by a multi-disciplinary team, which would include hydrologists, geomorphologists and ecologists. If a clear link between fluvial transport of sediment and seed can be shown theories and algorithms commonly used in fluvial geomorphology could be disseminated for better understanding of hydrochory (Groves *et al.* 2007). However, fluvial sediment transport models at the catchment scale, such as SedNet (Prosser *et al.* 2001), need to be modified to include life-history traits of species, including such factors as the difference in temporary storage capacity between the sediment and propagules. For instance, sediment may be 'temporarily' stored for hundreds of years, whereas most seed will be viable only for much shorter periods. However, the linking of these fields would accelerate our understanding of and capacity to model hydrochory.

Other areas for future research that have been highlighted within this thesis include the need to better understand better the spatio-temporal change in species richness and instream seed density during a flood cycle. How changes in river geomorphology can facilitate or impede seed deposition, plant germination and riparian vegetation structure. Is seed depletion of the seed bank occurring during flooding? Seed depletion may be modelled as a loop of synthesis similar to that of a sediment-limited river. Most seed are transported over a short period during a flood peak and so a better understanding of the dispersal dynamics over this period would improve predictability of the dispersal dynamics of hydrochorous plants.

Within this thesis I have developed a semi-empirical model that showed a good model fit to the data (Chapter 6), but it needs further development and calibration to establish the reliability of the coefficients across a wider range of flow regimes and landscapes. Furthermore, to understand better the movement of all fluvially dispersed seed, additional modelling needs to be carried out on propagules that either move suspended in the water column or saltate along the bottom of the channel, similar to the movements of suspended sediment and of the bedload. To make the model more holistic it needs to describe the full life cycle of fluvially dispersing species. This can be done through adding a population

matrix model, such as that described in Groves *et al*. (2007), and potentially an aerial dispersal model to estimate the seed rain that is being dispersed into the river channel.

7.8 Conclusions

This study has found a large number of species benefit from hydrochory to disperse, with the instream species pool varying through both time and space. The species that were dispersing were not found to be obligate hydrochorous species but used it as a method of dispersal by chance and geographic proximity to the channel. Instream seed composition had distinct differences between the sampling sites, indicating that most species disperse locally. Seed release experiments similarly showed that most seed were deposited near their release point. Water velocity was the main control of the dispersal kernel, although even at low flow a few outliers were capable of long distance dispersal. The Wingecarribee catchment was seed limited; the timing of release was the main factor that determined the instream pool species richness and seed density. However, the soil seed bank became a more dominant seed source during periods of low seed production and of high flow. Negative impacts from climate change and river regulation will reduce connectivity along rivers further isolating patches of native riparian vegetation. Hydrochory may be used to augment river restoration work and maintain the genetic continuality of otherwise isolated riparian vegetation patchers. Upstream connectivity and species pool are the most important factors that control fluvial seed pool composition and the river flow regime for their dispersal kernel, therefore it is possible to use hydrochory to aid restoration or maintain remnant patches of riparian vegetation, but to use this input of seed there is a need to know what is in the water.

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Appendix 1. Standing riparian vegetation species identified upstream (<5 km) from the six sampling sites, Wingecarribee catchment

Species	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
Acacia decurrens		x				
Acacia longifolia	x	x				
Acacia mearnsii		x				
Acacia parramattensis	x	x	x	x		
Acacia pravissima						x
Acacia rubida						x
Acer pseudoplanatus		x				x
Acetosella vulgaris	x		x	x		x
Adiantum aethiopicum		x				
Alternanthera denticulata	x	x	x	x	x	x
Anagallis arvensis	x	x	x			x
Anthoxanthum odoratum					x	x
Asperula conferta					x	x
Austrostipa ramosissima	x					
Avena barbata			x			
Bidens bipinnata	x					
Bidens pilosa		x				
Billardiera scandens var *scandens*		x		x		
Blechnum nudum		x		x		
Bracteantha bracteata		x		x		
Bromus catharticus	x		x	x	x	x
Bromus mollis						x
Bursaria spinosa	x	x				
Callistemon citrinus		x				
Callistemon sieberi	x					
Capsella bursa-pastoris	x		x			
Cardimine gunni subsp Y		x				
Carduus nutans				x		
Cardimine paucijuga	x		x			
Carduus tenuiflorus	x		x	x		
Carex gaudichaudiana					x	
Carex longebrachiata					x	
Casuarina cunninghamiana	x	x	x	x		
Cerastium glomeratum	x	x	x			x
Chamaesyce maculata	x	x	x	x		x
Cheilanthes austrotenuifolia		x				
Chenopodium Pumilio		x	x		x	x
Cirsium vulgare	x	x	x	x	x	x
Clematis glycinoides	x	x	x			x
Conium maculatum	x		x			
Conyza bonariensis	x	x	x			
Conyza albida		x				
Conyza bilbaoana		x				
Conyza canadensis	x	x	x	x	x	x
Conyza parva		x				

Appendix 1. continued

Species	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
Correa reflexa		x				
Crataegus monogyna					x	x
Cynodon dactylon						x
Cynoglossum suaveolens	x					
Cyperus difformis	x	x	x		x	x
Cyperus eragrostis	x	x	x	x	x	x
Cyperus lucidus	x	x	x	x		
Cytisus scoparius					x	
Dactylis glomerata	x	x	x	x	x	x
Dichondra repens	x	x	x	x		
Dipsacus fullonum subsp. *fullonum*					x	
Echinopogon ovatus	x					
Echium plantagineum	x	x	x	x		
Einadia nutans ssp. nutans	x					
Eleocharis sphacelata				x	x	
Epacris paludosa		x				
Eragrostis curvula	x					
Erigeron canadense		x				x
Erodium sp.	x	x	x			x
Eucalyptus bridgesiana	x					x
Eucalyptus cinerea				x		x
Eucalyptus elata	x					x
Eucalyptus fastigata				x		
Eucalyptus ovata			x		x	
Eucalyptus pauciflora		x		x		
Eucalyptus radiata		x				
Eucalyptus sieberi						x
Eucalyptus viminalis	x	x	x	x		x
Euchiton sphaericum					x	
Euphorbia lathyris	x		x			
Euphorbia peplus	x			x	x	
Foeniculum vulgare		x	x	x	x	x
Fumaria muralis	x	x	x			
Galinsoga sp.		x	x			x
Galium aparine						x
Geranium solanderi	x	x	x	x		x
Hakea eriantha		x				x
Hirschfeldia incana	x	x	x	x		
Holcus lanatus	x	x	x	x	x	x
Hypochaeris radicata	x	x	x	x	x	x
Isolepis cernua		x			x	x
Isolepis inundata	x	x	x	x	x	x
Juncus articulatus	x	x	x	x	x	x
Juncus sarophorus			x	x	x	x
Juncus subsecundus	x					
Lactuca sativa	x	x	x			x
Lactuca serriola	x	x	x	x		
Lavandula stoechas	x					
Leptospermum morrisonii		x		x		
Leptospermum obovatum	x		x	x		x

Appendix 1. continued

Species	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
Ligustrum sinense						x
Lolium perenne	x		x	x	x	x
Lomandra fluviatilis	x	x				
Lomandra longifolia	x	x	x	x	x	x
Lomatia myricoides	x	x				
Ludwigia peploides	x	x	x	x	x	x
Lycopus australis			x	x		
Marrubium vulgare			x			
Medicago lupulina					x	x
Melaleuca linariifolia		x				
Mentha x piperita		x				
Microlaena stipoides	x	x	x	x	x	x
Modiola caroliniana	x	x	x	x		
Myosotis sp.	x					
Nassella trichotoma	x		x		x	
Olearia viscidula	x	x				
Onopordum acanthium				x		
Orobanche minor	x					
Oxalis corniculata	x	x	x	x	x	x
Oxalis perennans	x	x	x			
Paspalum dilatatum				x	x	x
Persicaria hydropiper	x	x	x	x		x
Phalaris aquatica					x	
Phragmites australis	x	x	x	x	x	x
Phyllanthus tenellus		x				
Pinus radiata					x	
Plantago lanceolata	x	x	x	x	x	x
Poa annua		x	x		x	
Poa labillardieri					x	x
Poa pratense					x	x
Poranthera microphylla		x	x			
Prostanthera lasianthos		x		x		
Prunus domestica	x			x	x	x
Pteridium esculentum	x	x	x	x		x
Ranunculus ranunculus						x
Ranunculus repens			x		x	x
Romulea rosea		x				x
Rorippa palustris	x	x	x	x	x	x
Rosa rubiginosa			x			x
Rubus fruiticosus agg.	x	x	x	x	x	x
Rubus parvifolius	x	x	x	x		x
Rumex brownii	x	x	x	x	x	x
Rumex conglomeratus			x		x	x
Rumex crispus	x	x	x	x	x	x
Rumex obtusifolius					x	
Rumex pulcher					x	
Salix babylonica					x	x
Salix cinerea					x	
Salix fragilis					x	
Salvia reflexa						x

Appendix 1. continued

Species	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
Silybum marianum			x			
Sinapis arvensis			x			
Sisymbrium orientale			x			
Solanum nigrum	x	x	x			
Solanum pseudocapsicum	x		x			
Sonchus asper	x	x	x		x	x
Sonchus oleraceus	x					
Stellaria media	x	x	x			
Taraxacum sp.	x	x		x		x
Themeda triandra					x	
Tragopogon pratensis						x
Trifolium repens	x		x	x	x	x
Typha domingensis					x	x
Typha orientalis					x	x
Ulex europaeus				x	x	
Urtica urens	x	x	x	x		
Verbena bonariensis	x	x	x		x	x
Vicia sativa subsp *angustifolia*				x	x	x
Viola hederacea	x	x	x			
Viola odorata		x				
Poaceae 1	x					
Poaceae 2	x					
Poaceae 3	x					
Unknown 1	x					
Unknown 2	x					

Appendix 2. Species and their proportional abundance, sampled from the soil seed bank upstream (<5 km) from six sampling sites in the Wingecarribee catchment, southeastern Australia; species identification and counts from germination trials

	Relative occurrence per site						Total seed count	Relative occurrence per species
Species	1	2	3	4	5	6		
Alternanthera denticulata	0.1	0.3	1.4	1.5	0.0	1.8	45	0.90
Biden pilosa	0.0	0.1	0.0	0.0	0.3	0.0	2	0.04
Carduus nutans	0.0	0.0	0.0	0.0	0.0	0.1	1	0.02
Carduus tenuiflorus	0.6	0.3	0.0	0.0	0.0	1.2	19	0.38
Cirsium vulgare	0.1	0.0	0.1	0.0	0.0	1.0	10	0.20
Conyza bonariensis	5.4	4.6	17.7	7.7	7.2	13.4	473	9.46
Euchiton sphaericum	0.1	0.0	0.2	0.4	0.3	2.1	24	0.48
Gnaphalium americanum	11.3	11.7	6.0	4.2	11.3	6.5	422	8.44
Hypochaeris radicata	0.0	0.1	0.0	0.0	0.0	0.0	1	0.02
Sonchus asper	0.1	0.1	0.2	0.3	1.8	0.5	17	0.34
Taraxacum sp	0.0	0.1	0.1	0.4	0.0	0.0	5	0.10
Echium plantagineum	0.0	0.0	0.0	0.0	0.0	0.2	2	0.04
Rorippa palustris	0.0	0.9	0.7	1.2	0.3	0.2	28	0.56
Cerastium glomeratum	0.0	1.6	3.6	0.4	0.3	1.3	66	1.32
Petrorhagia dubia	0.0	0.0	0.0	0.0	0.0	0.7	6	0.12
Stellaria media	0.0	0.1	0.0	0.0	0.0	0.0	1	0.02
Casuarina cunninghamiana	0.0	0.1	0.0	0.0	0.0	0.0	1	0.02
Chenopodium ambrosioides	0.1	0.0	0.1	0.0	0.0	0.5	6	0.12
Einadia nutans ssp. nutans	0.0	0.1	7.5	4.9	3.8	4.8	167	3.34
Chenopodium Pumilio	0.0	0.0	2.6	0.0	0.0	0.1	26	0.52
Hypericum japonicum	0.0	0.0	0.0	0.4	1.3	0.0	8	0.16
Dichondra repens	0.0	0.0	0.0	0.0	0.0	0.1	1	0.02
Crassula sieberiana	0.2	1.2	0.7	0.4	6.2	2.2	66	1.32
Cyperus difformis	0.0	0.6	0.2	0.8	0.5	1.3	27	0.54
Cyperus eragrostis	1.3	3.6	0.7	1.4	1.5	2.5	93	1.86
Cyperus lucidus	0.0	0.0	0.0	0.0	0.0	0.6	5	0.10
Cyperus Luzula	0.0	0.0	0.2	3.1	0.0	0.6	31	0.62
Cyperus sphaeroideus	0.0	0.3	0.0	7.8	0.0	0.7	70	1.40
Eleocharis sphacelata	0.0	0.0	0.0	0.0	0.3	0.1	2	0.04
Isolepis inundata	0.6	2.2	3.0	4.9	1.5	5.2	144	2.88
Isolepis cernua	0.0	0.6	0.0	0.5	0.0	1.2	20	0.40
Isolepis gaudichaudiana	0.1	0.0	0.0	0.0	0.0	0.0	1	0.02
Euphorbia lathyris	0.3	1.5	0.0	0.1	0.0	0.0	19	0.38
Euphorbia peplus	0.7	17.2	0.8	0.0	0.0	1.0	192	3.84
Cytisus scoparius	0.0	0.2	0.0	0.0	0.3	0.0	3	0.06
Genista monspessulana	0.0	0.0	0.0	0.1	0.0	0.0	1	0.02
Medicago lupulina	0.0	0.0	0.0	0.0	0.3	0.0	1	0.02
Medicago polymorpha	0.1	0.0	0.0	0.4	0.0	0.2	6	0.12
Trifolium repens	1.9	1.8	5.2	2.3	10.8	2.5	170	3.40
Vicia sativa subsp angustifolia	0.3	0.3	0.2	0.0	0.0	0.2	10	0.20
Fumaria muralis	0.0	0.0	0.4	0.0	0.0	0.0	4	0.08
Erodium sp.	0.1	0.5	0.1	0.0	0.0	0.0	7	0.14
Geranium solanderi	0.0	0.0	0.2	0.0	0.0	0.0	2	0.04
Romulea rosea	0.0	0.4	0.0	0.0	0.0	0.0	4	0.08
Juncus articulatus	2.3	5.3	1.6	18.5	13.3	6.4	342	6.84

Appendix 2. continued

Species	Relative occurrence per site 1	2	3	4	5	6	Total seed count	Relative occurrence per species
Juncus capitatus	1.9	4.7	1.2	18.7	12.1	5.4	316	6.32
Juncus subsecundus	0.2	4.9	0.7	4.1	1.5	0.2	97	1.94
Juncus usitatus	58.6	18.7	3.7	1.7	3.1	2.9	877	17.54
Lycopus australis	0.0	0.0	0.0	0.0	0.0	0.1	1	0.02
Modiola caroliniana	0.0	0.0	0.2	0.0	0.0	0.0	2	0.04
Ludwigia peploides	1.0	0.4	0.6	3.6	5.6	4.2	105	2.10
Oxalis corniculata	0.5	0.8	1.2	0.5	1.5	2.5	56	1.12
Oxalis perennans	0.5	0.9	1.9	0.1	0.0	6.8	90	1.80
Oxalis pes-caprae	0.0	0.3	4.6	1.7	2.1	1.3	80	1.60
Plantago lanceolata	0.2	2.0	2.4	0.0	0.0	0.0	45	0.90
Bromus cartharticus	0.9	1.2	0.0	0.0	1.8	0.0	28	0.56
Bromus hordeaceus	0.0	0.0	0.0	0.1	0.0	0.0	1	0.02
Cynodon dactylon	0.0	0.0	0.0	0.0	0.0	0.6	5	0.10
Dactylis glomerata	0.0	0.3	0.0	0.0	1.3	0.0	8	0.16
Digitaria sanguinalis	0.0	0.0	22.7	1.7	3.8	0.0	250	5.00
Echinopogon ovatus	0.0	0.2	0.4	0.5	0.0	0.0	10	0.20
Holcus lanatus	4.5	1.5	0.8	0.1	1.3	0.7	82	1.64
Loliuim rigidum	0.5	0.0	0.0	0.0	0.0	0.0	5	0.10
Microlaena stipoides	0.0	0.0	0.0	0.0	0.0	1.7	14	0.28
Paspalum dilatum	0.0	0.5	0.0	0.0	0.5	0.0	7	0.14
Phragmites australis	0.0	0.3	0.0	1.3	0.0	0.0	13	0.26
Poa labillardieri	0.0	0.5	0.0	0.0	0.0	0.0	5	0.10
Poa pratense	2.3	0.2	0.0	0.0	0.0	0.0	26	0.52
Poa annua	0.0	0.2	1.5	0.6	0.0	0.0	22	0.44
Persicaria hydropiper	0.0	0.1	0.2	0.1	0.8	0.0	7	0.14
Polygonum aviculare	0.0	0.0	0.1	0.0	0.0	0.0	1	0.02
Rumex brownii	0.0	0.2	0.1	0.0	0.0	0.5	7	0.14
Rumex crispus	0.1	0.5	1.3	0.1	0.5	1.0	30	0.60
Pontederia cordata	0.1	0.0	0.0	0.0	0.0	0.0	1	0.02
Anagallis arvensis	0.2	0.8	1.3	1.9	1.5	2.8	67	1.34
Ranunculus repens	0.0	0.0	0.0	0.3	0.0	0.4	5	0.10
Ranunculus muricatus	0.0	0.0	0.8	0.0	0.8	1.9	27	0.54
Solanum nigrum	0.0	0.1	0.1	0.0	0.0	0.6	7	0.14
Verbena bonariensis	2.0	2.7	0.1	0.3	0.5	6.9	110	2.20
Xanthorrhoea resinifera	1.1	1.8	0.2	1.2	0.3	0.0	41	0.82
	20.76	19.66	19.54	15.64	7.802	16.58	4999	

Appendix 3. Species and their proportional abundance, sampled from aerial seed rain upstream (<1 km) from six sampling sites in the Wingecarribee catchment, southeastern Australia

Species	Relative occurrence per site				Total seed count	Relative occurrence per species
	1	2	3	4		
Acacia parramattensis	0.0	0.0	0.1	2.7	62	1.05
Capsella bursa-pastoris	0.0	0.0	0.1	0.5	13	0.22
Casuarina cunninghamiana	0.0	0.0	22.9	4.9	483	8.17
Cirsium vulgare	0.8	0.0	0.1	0.9	30	0.51
Conium maculatum	1.9	15.4	0.7	0.6	167	2.83
Conyza bonariensis	0.3	2.0	2.0	0.3	57	0.96
Conyza canadensis	0.5	18.1	7.8	0.3	279	4.72
Dactyli glomerata	18.2	6.8	15.8	10.5	778	13.16
Digitaria sanguinalis	0.2	0.1	4.0	1.5	103	1.74
Holcus lanatus	11.9	4.8	0.6	1.5	235	3.98
Hypochaeris radicata	8.4	26.1	8.2	0.4	452	7.65
Leptospermum morrisonii	2.3	0.0	5.4	36.3	919	15.55
Leptospermum obovatum	1.7	0.0	0.1	28.4	651	11.01
Paspalum dilatatum	35.8	10.4	2.3	3.1	650	11.00
Persicaria hydropiper	0.2	0.0	10.5	0.6	187	3.16
Phalaris aquatica	17.2	11.5	19.1	6.1	758	12.82
Rumex brownii	0.2	4.3	0.1	1.1	61	1.03
Rumex crispus	0.3	0.0	0.0	0.0	4	0.07
Solanum nigrum	0.2	0.5	0.4	0.0	14	0.24
Poaceae 1	0.0	0.0	0.1	0.2	5	0.08
Poaceae 2	0.0	0.0	0.1	0.0	1	0.02
Poaceae 3	0.0	0.0	0.0	0.1	2	0.03
	22.0	13.0	27.7	37.4	5911	